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THE ECOLOGY OF SOLITARY BEES[1]

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INTRODUCTION

MORE THAN 50 fruit and seed crops depend upon insect pollination for satisfactory yields. In recent years much progress has been made in the development of management procedures which make use of the introduced honey bee to increase agricultural production, particularly of legume seed crops grown in the southwestern United States. However, comparable management techniques have not been developed for the agricultural areas of northern and eastern United States, Canada, Scandinavia, northern Europe, and Russia (Åkerberg and Lesins, 1949; Peterson, 1954; Popov, 1951*b*, 1952*c*, 1956; Blagoveshchenskaia, 1954; Bohart, 1957; Hobbs, 1957; Medler, 1957).[3] As a result, considerable attention has been directed recently to the possibility of increasing the numbers of native species of bee pollinators (Bohart, 1947, 1957; Menke, 1952, 1954; Stephen, 1955; Blagoveshchenskaia, 1956; Medler, 1957; *et al.*) and suggestions have been made for improving the pattern of wild bee pollination by suitable introductions (Piper *et al.*, 1914; Larkin, 1952; Hurd and Michener, 1955; Bohart, 1957; *et al.*). The success of such programs depends upon a sound knowledge of bee ecology (Cumber, 1953). Some practical aspects of ecology of social bees (*Bombus*) have recently been reviewed by Cumber (1953) and Medler (1957) and of stingless bees by Schwarz (1948).

The present review is concerned with the environmental relationships of solitary bees, including ethological features of importance in their economy, survival, and evolution. No attempt has been made to develop historical aspects or floral ecology. In some cases only the later and more comprehensive papers have been cited, especially when these include bibliographical references to the earlier literature. Special attention has also been given to articles published in the last fifteen years, many of which have not yet been reviewed or commented upon. However, even within these limits, space will still not permit reference to hundreds of papers which have contributed to our knowledge of bee ecology as defined above. For convenience of reference, the taxonomic classification followed is essentially that of Michener (1944*a*).

[1] The survey of the literature pertaining to this review was completed in June, 1957. Received for publication November 21, 1957.

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[3] See "Bibliography" for citations referred to in the text by author and date.

GEOGRAPHICAL DISTRIBUTION

Size of Fauna. The bee fauna of the world is very large. Precise figures are not available but thirty-five years ago Friese (1923) estimated that bees represented more than one fourth (12,000 spp.) of the then known Hymenoptera (46,000 spp.). More recently, Stevens (1948) estimated that the total must be in the vicinity of 15,000; Michener (1955*b*) at about 19,000.

Ratio of Genera to Species. A characteristic of bees as a group is that the large numbers of species fall into relatively few genera. Friese (1923) recognized only 100 genera for an estimated 12,000 species. The most recent catalogue of bees for a major region of the world (Muesebeck, Krombein, and Townes, 1951) lists 99 genera and 3,287 species and subspecies in the portion of America lying north of the Mexican boundary. Of these, seven genera and about 400 species are social or semisocial and 26 genera and about 400 species are parasitic, leaving 66 genera and nearly 2,500 species of solitary nesting bees. Among the larger of these are *Andrena* (500+ spp.), *Perdita* (nearly 300 spp.), *Megachile* and *Melissodes* (each nearly 150 spp.), and *Osmia* (100+ spp.).

World Distribution and Regions of Abundance. Generally speaking, solitary bees are found throughout the world from the Arctic Circle to Tierra del Fuego and Tasmania, wherever flowering plants grow and suitable conditions exist for nesting. However, social bees of the genus *Bombus* are dominant in the higher latitudes (60° to 65°) of Scandinavia, Siberia, Alaska, and Canada (Friese, 1902; Sladen, 1919) and some species are circumpolar, differentiating subspecifically in various regions (Friese, 1935). Certain colletids (*Hylaeus*) and megachilids (*Osmia, Hoplitis, Heriades* and *Megachile*) which do not nest in the ground occur far to the north, and so do a few of the ground-nesting types (*Andrena, Melitta*) (Zetterstedt, 1838; Smith, 1853; Friese 1902). However, of 81 species or subspecies of bees considered by Friese (1902) to be arctic forms, only 46 (57 per cent) are solitary bees or their parasitic derivatives; the remainder (43 per cent) are *Bombus* (and *Psithyrus*). Thirty species of bees are now known for Alaska (Hurd, *in litt.*). Sixteen of these are *Bombus* (or *Psithyrus*), 11 are megachilids, three are *Andrena,* of which *A. clarkella* (Kirby) is Holarctic in distribution. In the Antipodes, the Chilean *Bombus dahlbomii* Guérin-Méneville and certain halictine species penetrate farthest southward (Malyshev, 1936).

Social bees also thrive in tropical regions (e.g. *Trigona, Melipona*), and of 353 species of bees recorded for Panamá by Michener (1954), 73 (21 per cent) are social Apidae (and parasitic derivatives). By contrast, only six species of *Bombus* are represented among the 439 species of bees now known from the semiarid locality of Riverside, California (Timberlake, *in litt.*). Damp tropical forests are generally unfavorable for ground-nesting bees and in regions of excessive humidity the endemic bees nest in a dry or protected substrate, as *Xylocopa, Megachile, Trachusa* (Malyshev, 1936). The greatest abundance of solitary bees is in the warm arid sections of the world having a semidesert character, especially western North America, Turkestan and adjacent regions, the Mediterranean basin, parts of South Africa, Australia, and western South America (Malyshev, 1936; Michener,

1940). Mountainous areas with moderate rainfall also offer varied floras and well-drained soil favorable to nesting. They commonly support abundant bee faunas.

Continental Distribution. Several genera of bees are more or less world-wide in distribution and have retained a remarkable degree of homogeneity in the course of their history. Such genera include *Hylaeus, Colletes, Halictus* (and *Sphecodes*), *Megachile,* and, to a slightly lesser extent, *Anthophora.* Others, such as *Nomia, Lithurge, Ceratina,* and *Xylocopa,* are more or less abundant and diversified in the warmer parts of both hemispheres. One genus, *Hesperapis,* has been found only in the arid regions of western North America and South Africa (Cockerell, 1936). A number of northern genera are primarily Holarctic, barely invading or poorly represented in the Southern Hemisphere. Included here are *Andrena* (and *Nomada*), *Panurginus, Macropis, Dufourea, Osmia, Chelostoma, Dianthidium.* Species represented in both the Old World and New World include at least two of *Andrena,* several each of *Osmia* and *Megachile,* and *Anthophora* (*Clisodon*) *furcata* (Panzer).

The southern continents have derived or retained certain large groups of their own, as the primitive Paracolletini. South America is characterized by the diphaglossine and chilicoline colletids, including *Ptiloglossa,* the large fauna of exomalopsine, emphorine and centrine Anthophorinae, the diversity of certain groups of Halictidae (as *Augochlora*), and the absence of the Melittidae. Africa is noted for the colletid genus *Scrapter,* the panurgines *Poecilomelitta, Meliturgula, Mermiglossa,* the halictine *Thrincostoma,* the xylocopine *Allodape,* and the Fideliidae,[4] and Australia, not only for the variety of genera and species of primitive, short and obtuse-tongued, skin-making bees (Colletidae) and the xylocopine genus *Lestis,* but also for the absence of certain groups, as the Panurginae. The New Zealand bee fauna is small and little known (Heine, 1937; Thomson, 1927) but has been supplemented by the successful introduction of bumble bees (Armstrong, 1883; Farr, 1886, *et al.*). As might be expected, the African bee fauna (Friese, 1909; Cockerell, 1936; Arnold, 1947) shows a definite Palearctic influence. It also exhibits numerous affinities with the Orient, as indicated by such groups as *Mesotrichia, Crocisa,* and *Nomioides* which occur also in southeastern Asia and Australia but are absent from the Western Hemisphere. The last is considered by Cockerell (1936) to be a halictine counterpart of the American panurgine genus *Perdita,* the species of which are similarly small and brightly colored. *Habralictus* is a Neotropical equivalent.

As might be expected, the larger genera of bees inhabiting Europe, Asia, and North America have rather broad and simple distributions with northern types dominating the northern continents, even south of the Himalaya Mountains (Bingham, 1897). Michener (1940) has characterized the situation in North America as follows: almost all bees north of approximately the Canadian border are northern types, those of the tropics are nearly all Neotropical, while those of intermediate regions, including most of the United States and the Mexican plateau, consist of a mixture of the two, the southern

[4] One species in this family has, however, been described recently from Chile (Moure and Michener, 1955).

forms decreasing toward the north, the northern toward the south. This generalized picture is nearly unmodified in the eastern half of the United States, where almost unaltered elements from both regions mingle, but in the west it is modified not only by varying topographic and climatic conditions which permit boreal faunas to extend southward along the mountain ranges, but also by the warm southern interior, contiguous with the climatically similar Mexican plateau, and forming with it a distinctive subregion, the Sonoran, combining arid phases of the Nearctic and Neotropical biotic regions, the Nearctic influence predominating within the United States.

The role of Panamá in the zoogeography of bees of the Western Hemisphere has been graphically described by Michener (1954). He emphasizes not only that the area must have been traversed by most of the groups of animals that have passed between the two continents, but also that groups are apparently still in the process of spreading along the Isthmus. Several Nearctic or Holarctic genera of bees (e.g., *Andrena, Calliopsis,* and *Heriades*) reach the southernmost limits of their known range near the Canal Zone. Since no major physiographic or climatic barriers exist between the southern limits of these groups and the broad expanses of the South American continent, Michener regards it as probable that these groups are recent arrivals, extending their way southward. Michener also states that a number of groups are absent from the lowlands of the Canal Zone region but occur at higher altitudes to the south and the north. Examples are several species of *Bombus* in the higher altitudes of middle America, including the mountains of Chiriquí Province, which are absent from the rest of Panamá, where altitudes are low, but reappear again at moderate altitudes in South America, and do not appear to be even subspecifically distinct. As a result, it is assumed that quite recently conditions similar to those of the 4,000-foot level of the Chiriquí area, extended more or less continuously from Chiriquí to Colombia.

Bees of Limited Areas. A further characteristic of bees is that within a given region a relatively small area may support a very large percentage of the known species. Although only some 3,200 species of bees have been recorded for America, north of Mexico, 439 species[5] have been collected at Riverside, California (Timberlake, *in litt.*), and nearly 300 at Carlinville, Illinois (Robertson, 1928). Hurd and Michener (1955) state that of 154 species in eight genera of North American megachiline bees studied by them, 116 species have been found in California and eight more probably occur, representing nearly 90 per cent of the species known from the Western Hemisphere. Likewise, of the 64 known species of *Dufourea,* 54 are found in California (G. E. Bohart, *in litt.*). Apparently bees are less numerous in southeastern United States where Michener (1947*b*) found 104 species near Hattiesburg, Mississippi, Graenicher (1930) only 65 in southern Florida. The relatively few genera of solitary bees, the relatively large number of species contained in most of these genera, and the high percentage of these species that can be found in certain areas suggest that the bees are a highly adaptive group and that presumably the reasons for their evolutionary success are to be found in their ecology.

[5] 117 of these represent undescribed species or subspecies.

Bees of Arid Regions. As has been emphasized above, the desert and arid areas of the world are particularly rich in bees, and the faunas concerned have had complicated derivations. With reference to North America, Michener (1940) has stated that the bees of the desert areas may be arbitrarily divided into two overlapping groups based upon their season of flight and the nature of the plants upon which they feed. The first of these consists of genera which, in the desert, fly primarily in the spring and are dependent upon the flowers of herbaceous mesophytes which grow and bloom during the short period when the desert is relatively moist. These are primarily Holarctic types (e.g. *Andrena, Dufourea,* and *Tetralonia*). The second group consists of genera which visit the flowers of the characteristic xerophytes, such as *Larrea, Prosopis,* and *Cercidium,* that bloom not only in the spring but also later in the year. The nearest relatives of these forms are Neotropical (e.g. *Centris, Ericrocis, Protoxaea* and apparently *Perdita*), or representatives of nearly cosmopolitan genera (e.g. *Halictus* and *Megachile*). Michener points out that there is scarcely a genus of bees every species of which may be unquestionably placed in one or the other of these groups, yet the division is quite evident.

In discussing a more restricted group (certain megachilid bees), Michener (1944*b*) has stated that with the exception of four groups, the American osmiine bees are northern and montane forms, rare in the deserts and virtually absent in the neotropics. The four exceptions, independently derived from northern forms, are characteristic of a zone in which they probably arose along the western margin of the desert of central and southern California.[6] Three of the groups are largely confined to this zone. The fourth, *Ashmeadiella,* has a broader range, covering most of North America, but is divisible into several subgenera, the distribution of which forms concentric areas whose common center is in the same region.

One of the most fascinating of zoogeographical questions involves the plant and insect groups common to the deserts of North and South America. On this subject, Michener (1954) has remarked that at least scattered desert areas must have once extended through Central and South America, presumably near the western shores. He notes that at the present time some of the promontories extending into the Pacific in the region of the Canal Zone exhibit quite xeric characteristics. Instead of being covered with jungle or grasslands (savanna), they support a tangle of large bushes and small trees (including mesquite, *Prosopis chilensis*) among which grow cactus plants. These localities are by no means deserts, but their vegetation suggests that they might become deserts if higher mountains or other factors reduced the rainfall of the Pacific side of Panamá.

Bees and Biotic Areas. Graenicher (1935) has discussed the distribution of bees in relation to biotic areas in Wisconsin, and Cockerell (1893) refers to the vertical distribution of bee species in a mountainous locality in Colorado. An informative analysis of bee distribution in relation to biotic areas has been provided by Hurd and Michener (1955) in their study of some megachiline bees in California. Making use of certain biotic areas outlined

[6] Some of these groups have since been shown to have a wider distribution (Michener, 1951*a*) than was at first believed to be the case, but these generalizations appear to be basically valid.

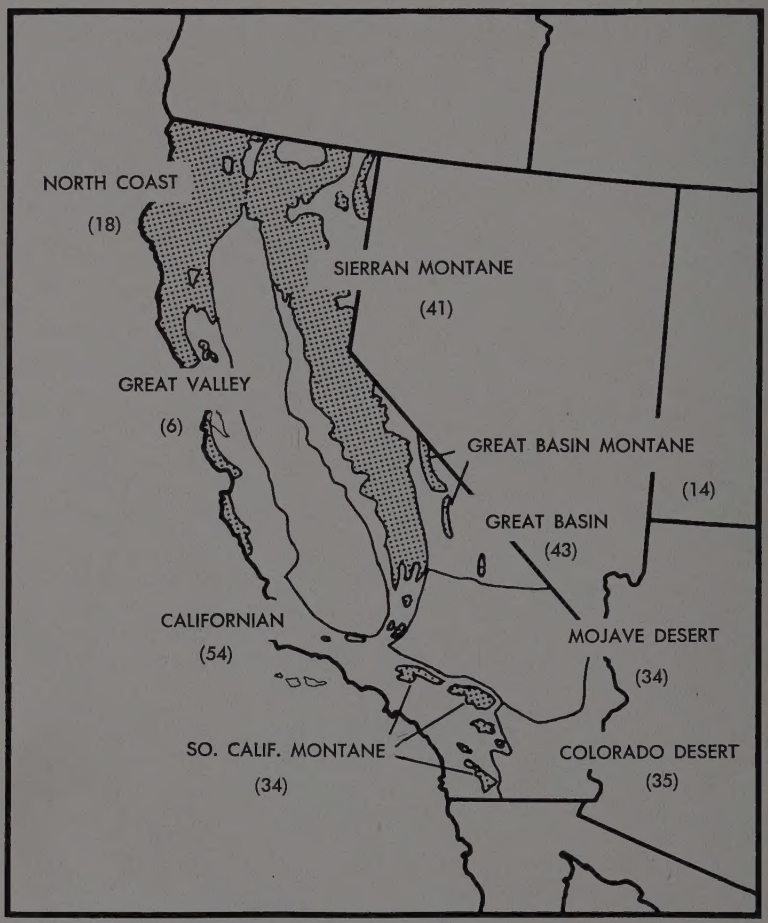


Fig. 1. Boreal (stippled) and Austral (white) areas of California showing biotic subdivisions occupied by the megachiline bees listed in table 1. Numbers indicate the number of species found in each district (after Hurd and Michener, 1955).

by Miller (1951), the number of species in each genus or subgenus occurring in these areas was tabulated (table 1) and recorded on a map (fig. 1). Their data reveal that some of the groups are wide ranging (e.g., *Ashmeadiella* s. str., *Alcidamea*), others more restricted (e.g., *Hoplitina, Acrosmia, Eremosmia*). However, no species were found in all the areas, many were restricted to specific areas. Commonly some species were entirely or principally found in the areas classed as boreal, or entirely or principally austral, although sometimes (e.g., *Anthocopa triodonta,* Cockerell) they straddled

this line. More important, perhaps, the austral species (presumably derived from boreal groups) are more abundant than the boreal. This is in agreement with the generalization expressed above that solitary bees as a group appear to find warmer and drier regions more favorable than warmer and moister or cooler and moister regions. Also, from these and other studies it seems probable that most bee distributions are determined more by broad climatic factors than by biotic areas.

Bees and Plant Communities. Graenicher (1930) has briefly discussed bees and plant communities in the Miami region of Florida, but without drawing any generally applicable conclusions. Pearson (1933) in a study of the ecological relations of bees in the Chicago region concluded that although there is a frequent preference for some community or community type, bees are to be thought of as "following" the flowers and as being probably secondarily adapted to the communities which they are thus led to frequent. He was only occasionally able to indicate a bee as a visitor to only two or three communities, yet he considered it feasible to present lists of bees to be expected in the various communities (table 2) at the proper seasons. He also concluded that certain families of bees are more characteristic of a given community than of another, the social bees (Apidae) and semisocial bees (Halictidae) being the least so. A broad study of bees in relation to the entomophilous vegetation and plant associations has been made by Popov (1952) in the State Forest region of Mt. Vishnevaya—Caspian Sea. More than 21,500 bees of 120 to 140 species were collected and classified according to 120 kinds of vegetation. Meadowland was richest in numbers of individuals and diversity of species, with wild or wastelands and forests least so. Species adapted to steppe vegetation were few and most of these penetrated into wastelands or other categories. Bees of the forest fringe area, although abundant, mainly involved species widely scattered through other zones or plant communities.

Dispersal of Introduced Species. Certain bees, especially those which nest in wood or plant stems, are subject to transport by man and have been accidentally introduced into various regions. Moure (1943) has reported the introduction and spread in Brazil of the European species *Anthidium manicum* (Linnaeus) which nests in wood, including furniture, and is now common in the state of São Paulo, visiting principally flowers of *Leonurus* and *Anthirrhinum*. All of the Hawaiian bees except those of the genus *Nesoprosopis* appear to have been introduced accidentally by man, including five species of *Megachile* and one each of *Xylocopa* and *Lithurge* (Williams, 1927). According to Timberlake (*in litt.*), one of the species of *Megachile* was probably introduced by the Polynesian people. *Andrena wilkella* (Kirby) appears to have been introduced into eastern North America where it is now common but is notably lacking from the local lists of fifty years ago and more. The best documented account of the establishment and spread of Old World species introduced into North America has been provided by Hurd (1954) for three species of the megachiline subgenus *Eutricharea* which have been established along the Atlantic seaboard, in the Great Plains states and in California. The species are not thought to be oligolectic, yet half of the plant species visited in the Great Plains area and half of those in Cali-

TABLE 1

DISTRIBUTION WITHIN CALIFORNIA OF SPECIES OF CERTAIN GENERA OF MEGACHILINI

(Numbers Indicate the Number of Species in Each Area)

(After Hurd and Michener, 1955)

Genera and subgenera	Calif. species	N. Amer. species	Boreal (in California)				Austral (in California)				
			North Coast	Sierran	S. Calif. montane	Great Basin montane	Great Basin	Mojave Desert	Colorado Desert	Californian	Great Valley
Heriades	3	13	1	1	3	..	1	..	..	2	..
Chelostoma	8	8	1	3	5	..	..	..	..	5	..
Chelostomopsis	1	1	1	1	1	..	..	..	..	1	..
Hoplitis											
Formicapis	1	1	..	1	..	..	..	..	..	..	..
Robertsonella	..	1	..	..	..	..	..	..	..	..	..
Hoplitina	6	6	..	..	..	..	3	3	1	3	..
Acrosmia	3	3	..	3	1	..	..	..	..	..	..
Alcidamea	7	9	2	3	3	2	1	..	2	5	1
Ancronicus	..	1	..	..	..	..	..	..	..	..	..
Cyrtosmia	1	1	1	1	1	..	..	1	..	1	..
Dasyosmia	2	2	..	..	..	..	2	1	1	..	..
Monumetha	3	4	2	3	2	..	..	..	..	2	..
Anthocopa											
Atoposmia	8	9	1	7	3	3	..	..	..	2	..
Eremosia	13	17	..	..	..	..	10	7	9	1	..
Hexosmia	2	2	1	1	1	1	..	1	1	2	..
Proteriades	22	22	2	6	5	3	5	5	5	9	..
Ashmeadiella s. str.	19	27	5	6	7	4	10	8	9	16	5
Titusella	1	3	..	1	..	..	1	1	..	1	..
Arogochila	11	15	1	4	2	1	5	4	2	4	..
Corythochila	2	2	..	..	..	..	2	1	2	..	..
Chilosima	1	2	..	..	..	..	1	1	1	..	..
Cubitognatha	1	1	..	..	..	..	1	1	1	..	..
Diceratosmia	1	4	..	..	..	..	1	..	1	..	..
Totals	116	154	18	41	34	14	43	34	35	54	6

TABLE 2

PREDICTIONS OF THE OCCURRENCE OF BEES IN VARIOUS PLANT COMMUNITIES IN THE CHICAGO AREA BASED UPON FLOWER RELATIONSHIPS OBSERVED BY ROBERTSON AT CARLINVILLE, ILLINOIS (AFTER PEARSON, 1933)

Community	No. of bee species predicted	No. abundant or frequent	No. of flower species visited	Ratio of flowers to bee species	No. of flower bee species visits
Sand dune and upland associations					
Beach	0	0	0		0
Fore-dune	46	9	4	1–11.5	61
Cottonwood	102	38	10	1–10.2	159
Pine dune	153	71	18	1– 8.5	344
Black oak	195	90	47	1– 4.15	668
Mesophytic oak forest	179	86	56	1– 3.19	854
Climax Mesophytic forest	130	49	47	1– 2.76	591
Sandy swamp	63	12	12	1– 5.25	119
Prairie association					
Low prairie	153	64	44	1– 3.47	615
High prairie	222	131	73	1– 3.04	1364
Aquatic associations					
Submerged aquatics	35	11	2	1–17.5	36
Floating-leaved aquatics	20	9	3	1– 6.66	27
Emergent aquatics	115	57	13	1– 8.84	283
Reed swamp	0	0	0		0
Sedge swamp	122	39	25	1– 4.88	383
Peat bog associations					
Sedge	90	22	10	1– 9.0	153
Xerophytic shrub	11	3	3	1– 3.66	12
Tamarack	52	8	3	1–17.3	56
Pine-birch forest	69	21	4	1–17.25	94
Rock ravine associations	43	9	5	1– 8.6	67
River cliff associations	189	103	34	1– 5.56	705
Flood-plain associations	223	137	120	1– 1.85	1698
Lake cliff associations	150	63	18	1– 8.31	337
Totals	2362	1032	551	1– 4.28	8616

fornia are of Old World origin. Unfortunately, data on the ecological impact of introduced solitary bees are virtually lacking. However, Pearson (1933) says that the honey bee in North America appears to exert an influence upon native bees, which is visible to any student of the native species. He states that it is so efficient a collector of pollen and nectar and so ubiquitous, that there can be no question but what its inroads cause a serious diminution in the food supply of native bees, particularly in unfavorable seasons.

Dispersal of Native Species. The development of agriculture has undoubtedly had a profound influence on the distribution of native bees. The cultivation of squash in North America has greatly increased the range of species of *Xenoglossa* and *Peponapis* (Linsley, MacSwain, and Smith, 1956*a;* Fronk and Slater, 1956), which were formerly limited to areas of native gourds such as *Cucurbita foetidissima.* Likewise, the world-wide cultivation of alfalfa (*Medicago sativa*) has undoubtedly increased the distribution of the local native bees associated with legumes or preadapted to make use of this plant [e.g. *Nomia melanderi* Cockerell, *Melitturga clavicornis* (La-

treille)]. Unfortunately, precise data are lacking and we can only speculate as to what must have happened in such cases. On the other hand, many agricultural practices also are known to be disadvantageous to native bees (Bohart, 1955) and have reduced their range by destruction of nesting sites.

Timberlake (*in litt.*) reports that the common *Lasioglossum stultum* (Cresson) of eastern North America has become established at Riverside, California, since he first began collecting there in 1924, and is now abundant. Since this species is also found in the Old World, it may have been introduced. Although the mechanism of dispersal in this case is not clear, *Lasioglossum* spp. are commmonly found in moving automobiles (G. E. Bohart, *in litt.*). In fact, the social halictines in general are widespread in distribution. For instance, the common *Halictus ligatus* Say, of southern Canada and the United States occurs at least as far south as Colombia. Among carpenter bees of the genus *Xylocopa,* recent extensions of range have been reported both in Europe (Haan, 1952; van Lith, 1955) and North America (Hurd, 1955; 1956). Hurd (1956) attributes local range extensions of *X. tabaniformis orpifex* Smith to the creation of suitable nesting sites in the form of structural timbers in areas previously unavailable to the bee. Westward extension of the range of an eastern North American ground-nesting solitary bee, *Melissodes bimaculata* Lepeletier, has been recorded by Cockerell (1938).

GENERAL BIOLOGY

The natural history and nesting habits of solitary bees fascinated many early students of insect biology (e.g. Réaumur, 1734–1742; Fabre, 1879–1907), and studies of this phase of bee biology reached a high level in the works of Malyshev (1936). Life history studies are still needed as many lacunae remain to be filled. However, such studies are most useful when written from the comparative, phylogenetic, or ecological points of view (Linsley, MacSwain, and Smith, 1952*c*; Michener, 1953*a*; Michener, *et al.*, 1955). The following summary relates to various phases of the natural history of bees which have ecological implications. Much of the information included is treated in greater detail by Pérez (1889); Friese (1891, 1923); Ferton (1923); Bischoff (1927); Nielson (1934); Caullery (1942); Michener (1944*a*); Hardouin (1948); Bohart (1953); Grandi (1951); and especially Malyshev (1936).

Mating Habits. In order to function as an isolating mechanism mating habits must be highly specific in a group as numerous in species as the bees. This appears to be generally the case. Some of the species which nest gregariously (e.g. certain anthophorines and panurgines), mate over the nesting site which is patrolled by the males while the females are active. In a few instances (e.g. some *Andrena* and *Paracolletes*), mating may take place in the burrow. Bohart (1950) has reported a situation in which males of several species of halictines were mating and attempting mating, sometimes indiscriminately, with females feeding on fermenting juices of watermelon. In most cases, however, mating occurs at or in the vicinity of flowers which the female is visiting for pollen, although in *Nomia melanderi* Cockerell it takes place both at the nesting site and at flowers. Males of this species have

most success in copulating with freshly emerged females whose wings are not strong enough for full flight, but they are sometimes so abundant on alfalfa flowers as to force females to forage half a mile away (G. E. Bohart, *in litt.*). In species with highly restricted pollen sources, male flower response may be as specific as that of the female (e.g. *Diadasia*). In species with a variety of acceptable pollen sources the males may have to range widely in search of females and the pattern is far less restricted (e.g. certain nongregarious *Anthophora*). Males of certain species of *Andrena* apparently patrol hedgerows and nonblossoming shrubs (Perkins, 1919), and Rayment (1935) records male flights of *Paracolletes facialis* Cockerell about tips of *Leucopogon* one to two weeks before the plants bloom. Rayment also reports the males of Australian *Trichocolletes* at *Hardenbergia* and *Hovea,* the females at *Daviesia* spp.

Copulation is usually very brief and difficult to observe, often lasting only seconds. However, in the Panurginae it is prolonged, and mating pairs are commonly encountered (Robertson, 1922; Rozen, 1958). In *Nomadopsis* males of some species seek the female at the nesting site and may ride to the flower site attached to her (Rozen, 1958); in others the reverse is true.

A phenomenon associated with mating in solitary bees is proterandry (Müller, 1882); Demoll, 1908; Robertson, 1918, 1930) or the emergence of males in advance of the females, presumably to assure immediate fertilization. In certain groups which arrange their cells end to end (e.g. *Osmia*), males sometimes develop in the outermost cells to facilitate this timing. Although there is no doubt of the early emergence of males of certain species of bees, most data gathered in relation to proterandry have been taken from observations or collections made at flowers. Actual emergence data from the nesting site of *Andrena erythronii* Robertson does not support the conclusion that it is proterandrous in emergence, although the males precede the females in activity about the flowers (Michener and Rettenmeyer, 1956). However, proterandry is definite in *Nomia melanderi* Cockerell and is reflected in earlier pupation and transformation in the cells as well as in flight (G. E. Bohart, *in litt.*). In any event, the male season in solitary bees is usually considerably shorter than that of the female (Robertson, 1918; 1930).

Robertson (1922) in discussing proterandry in the Panurginae considered that all of the local species were proterandrous but pointed out that the males apparently precede the females by so few days that this was difficult to establish, and his flower records yielded nearly twice as many females as males.

Selection of the Nesting Site. The most important limiting factors involved in suitable nesting sites appear to be a satisfactory substrate, proximity of appropriate sources of pollen and nectar, and in some cases nearness to water (e.g. many anthophorines) or plants with certain types of leaves, fibers, mud, or resins (e.g., most megachilids). However, a great many solitary bees return to the site from which they emerged and construct their nests near those of their parents. Among ground-nesting forms this sometimes ultimately results in extensive aggregations involving thousands of nests (e.g. certain *Andrena, Dasypoda, Anthophora,* and *Nomia*), but usually

the resultant groups are much smaller, and gregarious tendencies less well marked (Malyshev, 1936). In some cases, however, new sites may receive populations of 100,000 females or more within a few days in *Nomia melanderi* Cockerell and *Nomadopsis scutellaris* (Fowler) (G. E. Bohart, *in litt.*).

Most solitary bees nest in the ground. Depending upon the species, a preference may be exhibited for loose or hard-packed, sandy, or clay-like soil. Most bees avoid areas which are gravelly or rocky or where the vegetation, especially grass, is dense, but some regularly select rocky soil. Many prefer open-bare ground (e.g., many *Nomia*), others the edges of woods or glades (e.g., some *Andrena, Panurgus, Systropha*). Still others nest under the protection of a dead leaf, stone, or piece of wood. *Callomelitta picta* Smith constructs its burrows in punky wood instead of soil (Rayment, 1935). Nearly all prefer fairly well-drained sites and certain species of *Anthophora* and *Colletes* regularly select banks (including man-made walls of mud and adobe bricks). *Megalopta ipomoeae* Schrottky, a nocturnal bee, has been found nesting in moist ground in the semidarkness of a tropical forest (Jörgensen, 1912; Malyshev, 1936). Various other bees also nest in moist soil but avoid areas with poor surface drainage (Bohart, 1955).

Among the groups which regularly nest in plant materials (many *Hylaeus, Ceratina, Xylocopa,* most smaller Megachilini, but including some *Megachile*), some utilize plant stems (as bramble, raspberry, teasel, mullein, bamboo, et cetera), others burrow into the pith or soft heartwood of dead twigs and branches (as elderberry, maple, ash, et cetera), a few nest in galls, cones, or fruits. In most cases an existing hole or crack is necessary to provide access into the stem or branch, and the bees then excavate the softer materials. Most species of *Xylocopa* and the anthophorine subgenus *Clisodon* gnaw out tunnels in solid wood.

Preëxisting cavities are utilized by many megachilids and species of *Hylaeus* and these may include beetle burrows in wood or bark, deserted nests of anthophorine bees and mud wasps, snail shells, or such man-made cavities as nail holes, key holes, et cetera. A few bees (*Chalicodoma, Euglossa*) construct their nests in exposed or only partially enclosed areas such as large cavities in stones, under overhanging cliffs, beneath roofs or buildings, et cetera. Species of *Dianthidium* attach their nests to exposed rocks or plant stems.

Nest Construction. Malyshev (1936) has given a full account of the preparation of the nesting site by various solitary bees. Certain features having special ecological significance should be mentioned here. Many ground-nesting species pile the excavated soil from their burrow about the entrance in a characteristic hillock or tumulus. These tumuli are often quite conspicuous, and, incidentally, provide recognition landmarks for parasites and predators, especially bombyliid flies which flick their eggs into the entrance. Others (certain *Nomia, Anthophora, Diadasia, Eucera,* et cetera) construct an entrance tube or turret. These vary greatly in form and structure and have been regarded by some as a means of protecting the entrance from rain or to prevent certain types of parasitism. However, in many species the turrets have dorsal gaps which would seem to minimize any such functions. Since turrets are most common among groups of bees in which

gregarious nesting is prevalent, they may have some social significance. Emlen (1952) associates the retort-shaped nest of the cliff swallow with intense local territorialism.

The main shaft also varies in length and in shape from species to species. Those forms which nest in ground covered by vegetation (e.g. *Xenoglossa fulva* Smith) apparently dig deep to avoid plant roots. Those that nest in sandy, well-drained desert soils (e.g. *Andrena mojavensis* Linsley and MacSwain) apparently sink a deep shaft to the appropriate moisture level. The number and arrangement of cells are also variable. Some colletids, the xyclocopines, and most of the anthophorines and megachilids place the cells end to end in a regular series and, except for the first, emerging bees must escape through the cell above. Some colletids, the andrenids, dufourines, and melittids construct separate cells at the end of short tunnels off the main shaft.

The cells may be formed by hollowing out the end of a burrow or, as in many anthophorines, they may be built into the excavated cavities and can be removed intact during excavation. Various intermediate conditions also exist and have been fully discussed by Malyshev (1936). The cells and sometimes the tunnels of the colletids are lined with a thin transparent cellophane-like material. In the more primitive colletids the cells are usually separate, at the ends of individual tunnels (Janvier, 1933; Rayment, 1935; Michener and Lange, 1957), in *Colletes* they are more commonly arranged in series. In most of the other solitary bees except the megachilids, the cells are lined with a thin layer of wax-like or varnish-like waterproofing material. These secretions are salivary in the case of colletids, andrenids, and halictids, abdominal in some anthophorines (G. E. Bohart, *in litt.*). The cells of the Megachilidae are not constructed from the substrate but are made from foreign materials. Most *Megachile* utilize leaves or sections cut from leaves, or flower petals and sepals, but some use mud or pebbles with or without leaves. *Trachusa* uses leaf sections cemented together with resin or gum, *Heteranthidium* sand cemented with resin, *Dianthidium* and *Chelostomoides* pebbles cemented with resin, *Serapista* plant fibers attached to trees, *Callanthidium* and *Anthidium* plant down in cavities in the ground, plant stalks or wood. *Callanthidium* plugs its burrow with sand and resin, *Anthidium* with small stones. The habits of *Osmia* are quite varied, some using mud, others masticated leaf material, others the two combined, and still others resin.

The cells are provisioned with pollen and usually also with nectar. In the Andrenidae, Melittidae, and certain others the nectar added is sufficient to make the pollen dough-like and it is molded into a ball. In other cases it is stored quite dry (*Lithurge*) or with a coating of dry pollen (certain smaller Megachilini). The colletids and many anthophorines provide a rich mixture of nectar and the food store may be semiliquid or gruel-like. In *Tetralonia malvae* (Rossi), gruel-like provisions are covered with a thin layer of transparent honey (Malyshev, 1936). For most *Anthophora* about one half of the food is liquid. The larva utilizes this up to the final instar when it consumes the solid material (G. E. Bohart, *in litt.*).

Lithurge fuscipennis (Lepeletier) oviposits in a pocket in the pollen during the process of securing the provisions (Malyshev, 1930), as do certain species of *Osmia* (G. E. Bohart, *in litt.*) but, in so far as known, other solitary bees lay their eggs after provisioning is complete. Depending upon the group, the position of the egg is usually quite characteristic. Usually it is placed on the provisions attached by one or both ends or floating if the texture of the material requires. However, *Ceratina* attaches the egg to the side wall of the cell so that it is partially covered by the pollen (Malyshev, 1936), certain *Osmia* insert the egg partially into the pollen, and the North American emphorines place the egg beneath the stores (Linsley, MacSwain, and Smith, 1956*b*). *Colletes* attaches the egg to the cell wall away from the food, as do the parasitic Anthophorinae (e.g. *Melecta, Nomada*).

Jacobs (1924) points out that females of most solitary bees possess integumentary scent glands. Originally functioning as a sex attractant, they apparently provide a distinctive nest odor in *Mesotrichia* (Skaife, 1952) and probably other bees.

Development and Overwintering. After oviposition the cell is sealed, often with a flat disk of mud, spirally ridged internally. When the larva hatches it feeds on the stored provisions, grows rapidly, passes through an uncertain number of instars, and usually requires a few weeks to complete development, but in *Nomia melanderi* Cockerell development from egg to full grown larva may require as little as eight days (G. E. Bohart, *in litt.*). Megachilids void feces very early in larval life (Michener, 1953*b*; van Lith, 1957) and during the last instar frequently weave them into the fabric of the cocoon. Other bees defecate on the cell walls but, at least in some cases, only after full larval growth. However, there are some exceptions (Linsley, MacSwain, and Smith, 1956*a*). This developmental sequence usually is followed by a diapause during which the bee is very resistant to alterations in the physical environment. Among bees with a single annual generation this diapause usually lasts for the major part of the year, and under conditions unfavorable to bee activity it may extend over two or more years. This is the overwintering stage for most solitary bees. It is followed in the spring by a brief period prior to pupation and emergence during which the larva is active but nonfeeding. *Andrena* and most *Osmia*, however, transform in the fall and overwinter in the natal cell as unemerged adults. Among species of *Xylocopa* and *Ceratina* larval diapause is apparently short, evanescent, or nonexistent, and development is direct, the mature adults emerging and overwintering gregariously in old burrows or hollow stems. [Friese (1901) records the overwintering of *Xylocopa* in abandoned burrows of Anthophora.] In general, solitary bees, other than megachilids, do not construct a cocoon (*Macropis, Systropha,* and emphorine Anthophorinae are among the exceptions). The Megachilidae spin mammillate cocoons which have considerable phylogenetic significance, and various subgroups in the family may be distinguished by the degree of development of the apical nipple. Among halictine bees, at least in cold climates, males emerge in the summer and fall, mate and then die, only the females overwintering. Even in southern California only females of most species may be found from January to May (Timberlake, *in litt.*).

Sleep. Nesting females generally spend the night in their burrows and usually bar other individuals by means of a plug. Some males (e.g. many panurgines) curl up in the center of a flower [Banks (1908); Lieftinck (1957)], or, along with non-nesting females, may use emergence holes or deserted burrows (e.g. some *Andrena*) or may dig temporary burrows for night shelter (e.g. some *Nomia* and *Anthophora*). In *Nomia* several hundred males have been found in a single pocket (G. E. Bohart, *in litt.*), in *Osmia* they sometimes gather in cracks (Hirashima, 1957), and in *Anthophora* the burrows may be used gregariously by both sexes or even by host and parasitic bees (Linsley, 1943). Males of many solitary bees spend the night congregated in large number (Buttel-Reepen, 1915). Certain species of *Eucera, Chelostoma,* and *Anthidium* grasp a stem with the mandibles and rest with the body extended in the manner of sphecids (Friese, 1923). Both sexes of *Coelioxys* grasp the stem with the mandibles with the body upside down and the legs tucked in closely (G. E. Bohart, *in litt.*). *Svastra, Melissodes,* and *Exomalopis* grasp the stem with all six legs as well as the mandibles (Schwarz, 1901; Rau, 1916) and may be oriented with the head up as in *M. bimaculata* (Lepeletier) (Banks, 1908) or down as in *S. obliqua* (Say) and *M. perplexa* Cresson (Mathewson and Daly, 1955). According to Rayment (1935) the jaws of sleeping bees may clamp so tightly in such cases that large raindrops striking the body will decapitate the bees. Mixed aggregations of sexes and even species have been recorded as sleeping together by Banks (1908), Rau (1916), and Rayment (1935). The latter reports males and females of *Anthophora saltera* Cockerell, *A. cinctofemorata* Cockerell, and *Asaropoda punctata* Rayment together on the same stems. Rayment also records from Australia large nocturnal clusters (100 to 300 males) of various species in the genera *Paracolletes, Heterocolletes, Stenotritus,* and *Nomia,* on leaves and in bracken fronds. Similar aggregations of eucerine bees have been observed in Perú (E. S. Ross, *in litt.*) and of *Nomia* in Java (Lieftinck, 1957). Rayment found that the temperature is increased by this clustering, and Grassi (1942) considers gregarious sleeping a possible stage in the evolution of social habits.

Matinal and crepuscular bees sleep in the day time. Thus, males of *Xenoglossa* and *Peponapis* spend the day in flowers of *Cucurbita* (Bradley, 1919); Linsley, MacSwain and Smith, 1956*a*).

FOOD HABITS AND FLOWER RELATIONSHIPS

All species of bees are dependent upon flowers for their basic food. As with most organisms, food habits have played an important role in their evolution and speciation. The choice of larval food, as is usually the case with plant-feeding insects, is made by the adult. The larval food is pollen, usually mixed with some nectar, gathered from flowers by the female bee. However, bees may visit flowers for a variety of reasons, other than pollen collecting (Taniguchi, 1956). Flowers provide adult food (nectar and some pollen), the site of mating for many species, and a sleeping place for others. The collection of pollen by females invokes the most consistently specific response to flower species, although in some cases the mating search by males may be equally specific.

The broad subject of the interrelations of flowers and insects has been primarily the concern of botanists (e.g. Kölreuter, 1761; Sprengel, 1793; Delpino, 1867; Hildebrand, 1867; Müller, 1873; Kerner, 1876; Plateau, 1877, 1895; Knuth, 1898–99; Kirschner, 1911; Lovell, 1918; Knoll, 1921–1926; Clements and Long, 1923; Robertson, 1928; Graenicher, 1935; Grant, 1950; *et al.*). Some of these students have made substantial contributions to entomology and to bee ecology, but by and large the majority have approached the problem from the standpoint of floral ecology. Thus, Sprengel (1793) is credited with being the first to attach significance to flower color, scent, and form from the viewpoint of their relation to insect pollination. Subsequently Darwin (1859) gave impetus to the investigation of this aspect of the problem by emphasizing the importance of cross pollination. Müller attempted to apply the Darwinian theory of evolution to flowers and the insects which visit them in a series of important papers which culminated in his classical work on the fertilization of flowers (1873), the basic reference work for students of pollination. Grant (1949) has provided an informative and up-to-date discussion of the role of insects, especially bees, in relation to pollination systems, evolution, and speciation among angiosperms.

Near the turn of the century, entomologists began to contribute substantially to the knowledge of the interrelationships of bees and flowers, especially in parts of North America and Europe. However, important papers also appeared on the flower relationships of South American species, especially of Argentina (Jensen-Haarup, 1907, 1908; Jörgensen, 1909, 1912*a*, 1912*b*); Brazil (Ducke, 1901, 1902; Schrottky, 1901; von Ihering, 1905), Amaral (1953), and Paraguay (Schrottky, 1908, 1909; Bertoni, 1911). Recent contributions to the subject have been largely a by-product of thorough taxonomic treatments of various groups of bees (e.g. Timberlake, 1954, 1956) or life history studies (e.g. Michener and Rettenmeyer, 1956; Linsley and MacSwain, 1958*a*, *b*), and considerable light has been shed on certain aspects of the problem, especially flower constancy, by research workers in fields of agriculture such as orchard management (e.g. Brittain, 1933; Phillips, 1933; Butler, 1945), legume seed production (e.g. Linsley and MacSwain, 1947; Bohart, 1957; Popov, 1951*b*, 1952*c*, 1956), and contamination of vegetable seed crops (e.g. Bateman (1947); Crane and Mather (1943)).

Flower Constancy. Constancy in the collection of pollen is a characteristic of bees in general. Two types are involved. The first is characteristic of individual bees which, on one or several successive trips may gather pure (or nearly pure) loads of pollen from one kind of plant, although the species as a whole may be polylectic and not sharply limited in the kind and number of pollen sources utilized. This kind of constancy has long been known to floral biologists, students of insect behavior, apiculturists, and research workers in certain production aspects of agriculture. It is characteristic of social bees (e.g. *Apis, Bombus, Melipona*), semisocial bees (e.g. *Halictus*), and many solitary bees (e.g. some *Anthophora, Andrena, Megachile*). Plateau (1902) has described errors, largely by *Apis* and *Bombus*, in visiting flowers, and Bateman (1951) has discussed discrimination between species and varieties of *Brassica*. However, samples from bees with mixed loads may be 95 to

99 per cent pure (Grant, 1950), and may result from accidental contamination while visiting other flowers for nectar.

The second kind of constancy was partially recognized by Loew (1884) and was more clearly defined by Robertson (1925).[7] It is adaptive in nature and is characteristic of species, genera, and even higher groups of bees. This form of flower constancy is oligolecty, and is usually reflected in physiological and morphological adaptations which sharply limit the number and kind of pollen sources normally utilized by bees with this inherited characteristic. However, the term is relative and should be used accordingly (Popov, 1956; Linsley and MacSwain, 1958*a*, *b*).

The general subject of flower constancy has been comprehensively reviewed by Grant (1950) and certain phases have been discussed recently by Popov (1952*a*, 1952*b*, 1956) and Michener (1953*a*, 1954). The latter author comments on difficulties associated with the definition of the term oligolecty. The definition here adopted is that of Linsley and MacSwain (1958*a*). These authors define as oligolectic those species in which the individual members, throughout the range of the population, and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local absence of the pollen. Monolecty, as defined by Robertson (1925), usually results from a monotypic plant genus or from a single species of a plant genus occurring in the region occupied by the bee; it thus does not appear to differ from oligolecty.

Oligolectic species usually exhibit physiological adaptations to the host flower, such as short seasons more or less synchronized with the blooming period of the plant; frequently, daily flight periods coinciding with special diurnal periods of pollen availability; sometimes psychological adaptations to certain flower colors; in some cases cryptic coloration matching the flower; and often morphological adaptations for the extraction or transport of the pollen or to facilitate the simultaneous extraction of nectar from the pollen plant. However, Popov (1956) states that certain "relict" genera of bees (e.g. *Xylocopa*) are almost completely unadapted to pollination of modern flowering plants, but Nishida (1958) has demonstrated that carpenter bees are certainly adapted to pollination of flowers of the passion vine. Although Werckmeister (1951) records *Xylocopa violacea* Linnaeus as an assiduous worker of bearded iris (*Iris germanica*), interfering with plant breeding, and the chief pollinator of the little iris (*Hermodactylus tubersosus*) in the Mediterranean region, he also regards it as the primary factor in seed set of *Wistaria chinensis* and everlasting pea (*Lathyrus odoratus*).

Oligolectic Bees. Malyshev (1936) considers the great majority of solitary bees to be more oligolectic or monolectic than polylectic. He cites as examples

[7] Loew (1884) observed differences in the flower visiting habits of bees with tongues of about equal length (thus presumably with the same nectar sources available) and designated *monotropic*, *oligotropic*, and *polytropic* types, depending upon whether they visited a single species of plant, related species of plants, or unrelated plants, respectively. At first, Robertson (1899) adopted Loew's terminology but limited the application of the terms to flower visits for pollen. Later he proposed the parallel terms *monolectic*, *oligolectic*, and *polylectic* for use in reference to pollen visits of bees, restoring Loew's terminology to its original meaning (Robertson, 1925).

TABLE 3

OLIGOLECTIC BEES OF CARLINVILLE, ILLINOIS
(After Robertson, 1926)

Oligolege	Pollen source
Colletes aestivalis Patton	*Heuchera hispida*
albescens Cresson	*Petalostemum purpureum*
robertsonii Dalla Torre	*Petalostemum purpureum*
brevicornis Robertson	*Specularia perfoliata*
latitarsis Robertson	*Physalis*
willistonii Robertson	*Physalis*
armatus Patton	Astereae
americanus Cresson	Astereae, Heliantheae
compactus Cresson	Astereae, Heliantheae, Helenieae
Gnathosmia georgica (Cresson)	Astereae, Heliantheae, Cinchorieae
Ashmeadiella bucconis (Say)	Astereae, Heliantheae
Sayapis policaris (Say)	Heliantheae
pugnata (Say)	Heliantheae, Cynarieae
sayi (Cresson)	Heliantheae, Cynarieae, Eupatorieae
Megachile sexdentata Robertson	Heliantheae, Astereae
strophostylis Robertson	*Strophostyles helvola*
generosa Cresson	Leguminosae
Sarogaster georgicus (Cresson)	Papilionaceae
Anthidium psoraleae Robertson	Papilionaceae
Oligotropus campanulae Robertson	*Campanula americana*
Trachandrena spiraeana Robertson	*Aruncus sylvester*
mariae Robertson	*Salix*
Andrena erythrogastra (Ashmead)	*Salix*
illinoensis Robertson	*Salix*
macoupinensis Robertson	*Salix*
nigrae Robertson	*Salix*
salicacea Robertson	*Salix*
salicis Robertson	*Salix*
salictaria Robertson	*Salix*
arabis Robertson	Cruciferae
nothoscordi Robertson	*Nothoscordum striatum*
nubecula Smith	Astereae
Pterandrena asteris Robertson	Astereae
solidaginis Robertson	Astereae
helianthi Robertson	Astereae, Heliantheae
aliciae Robertson	Heliantheae
pulchella Robertson	Heliantheae
rudbeckiae Robertson	Heliantheae
krigiana Robertson	*Krigia amplexicaulis*
Ptilandrena erigeniae Robertson	*Claytonia virginica*
g. maculati Robertson	*Geranium maculatum*
polemonii Robertson	*Polemonium reptans*
Opandrena ziziae Robertson	Umbelliferae, zizioid
Iomelissa violae Robertson	*Viola*
Parandrena andrenoides (Cresson)	*Salix*
Chloralictus nymphaearum (Robertson)	Nymphaeaceae
Macropis steironematis Robertson	*Steironema*
Halictoides marginatus (Cresson)	*Helianthus*
Anthemurgus passiflorae Robertson	*Passiflora lutea*
Pseudopanurgus compositarum (Robertson)	Astereae
asteris (Robertson)	Astereae, Heliantheae
solidaginis (Robertson)	Astereae, Heliantheae
alibitarsis (Cresson)	Heliantheae
labrosiformis (Robertson)	Heliantheae
labrosus (Robertson)	Heliantheae
rudbeckiae (Robertson)	Heliantheae
rugosus (Robertson)	Heliantheae
Perdita octomaculata (Say)	Astereae, Heliantheae

TABLE 3—*Continued*

Oligolege	Pollen source
Perditella boltoniae Robertson	*Boltonia asteroides*
Zaperdita maura (Cockerell)	*Physalis*
Verbenapis verbenae (Cockerell and Porter)	*Verbena*
Calliopsis coloradensis Cresson	Heliantheae, Astereae
Melissodes cnici Robertson	*Cirsium*
coreopsis Robertson	*Coreopsis palmata*
vernoniae Robertson	*Vernonia fasciculata*
vernoniana Robertson	*Vernonia fasciculata*
asteris Robertson	Astereae
agilis Cresson	Astereae, Heliantheae
autumnalis Robertson	Astereae, Heliantheae
trinodis Robertson	Astereae, Heliantheae, Helenieae
boltoniae Robertson	Astereae, Heliantheae, Helenieae, Cichorieae
simillima Robertson	Astereae, Helenieae
coloradensis Cresson	Heliantheae, Cynarieae
Epimelissodes illinoensis (Robertson)	Heliantheae
atripes (Cresson)	*Cassia chamaecrista*
Anthedon compta (Cresson)	*Oenothera biennis*
Peponapis pruinosa (Say)	*Cucurbita pepo*
Xenoglossa strenua (Cresson)	*Cucurbita pepo*
Tetralonia atriventris (Smith)	Papilionaceae
robertsonii Cockerell	Papilionaceae
Cemolobus ipomoeae (Robertson) (ol.?)	*Ipomoea pendurata*
Melitoma taurea (Say)	*Ipomoea*
Emphor bombiformis (Cresson)	*Hibiscus*
Amegilla walshii (Cresson)	*Cassia chamaecrista*

of monolectic species *Andrena florea* Fabricius which collects pollen only from *Bryonia alba,* and *Macropis labiata* (Fabricius) which is restricted to *Lysimachia vulgaris,* and as oligoleges, *Tetralonia malvae* Rossi which gathers pollen from *Lavatoria thuringiana* or *Althea officinalis, Meliturga clavicornis* (Latreille) which collects from *Melilotus officinalis* or *Medicago sativa,* and *Melitta leporina* (Panzer) which takes pollen from *Medicago falcata, Melilotus officinalis* or *Trifolium montanum.* Other species are listed for Middle Asia by Popov (1956). The most complete account of the oligolectic bees of a region of North America has been provided by Robertson (1926). His list (table 3) for Carlinville, Illinois, is of interest as an example of what might be expected in a nonarid, temperate locality. This list exhibits oligolecty at the group level (*Sayapis, Pterandrena, Pseudopanurgus, Melissodes*) as well as at the species level.

Some oligolecty is evident at the family level, e.g., generally speaking anthophorine and megachilid bees choose a different series of flowers from the colletid and andrenid bees. At the generic level it is well illustrated by the species of *Macropis* (Malyshev, 1936; Michener, 1951*b;* Popov, 1956), *Chelostoma* (Michener, 1938) and *Proteriades* (Timberlake and Michener, 1950; Hurd and Michener, 1955). The species of the first group gather pollen only from flowers of *Lysimachia* and *Steironema* (Primulaceae), the second from Hydrophyllaceae, principally *Phacelia* and *Eriodictyon,* and the third group only from *Cryptantha* (Boraginaceae). Until recently, twenty-two species of *Proteriades* were known; all of these occur in California and

TABLE 4

OLIGOLECTY IN SOME SUBGENERA OF PERDITA
(Compiled from Timberlake, 1954, 1956)

Subgenus	Pollen source	Plant family	Bee species
Xerophasma	*Oenothera*	Onagraceae	2
Macrotera	*Opuntia*	Cactaceae	3
Macroteropsis	*Opuntia*	Cactaceae	1
	Sphaeralcea	Malvaceae	3
Heteroperdita	*Coldenia, Heliotropium*	Boraginaceae	7
Glossoperdita	*Gilia* (s.l.)	Polymoniaceae	3
Hesperoperdita	*Lotus*	Leguminosae	3
Cockerellia	*Verbesina*	Compositae	3
	Helianthus	Compositae	3
	Geraea	Compositae	1
	Baileya	Compositae	1
	Pectis	Compositae	1
	Coreopsis	Compositae	1
Procockerellia	*Stephanomeria*	Compositae	2
Pentaperdita	various genera	Compositae	4
Hexaperdita	various genera	Compositae	22
Pygoperdita	*Eschscholtzia*	Papaveraceae	7
	Calochortus	Liliaceae	9
	Eschscholtzia and *Calochortus*	Papaveraceae, Liliaceae	2
	Layia, Malacothrix, et cetera	Compositae	5
	Fallugia, Cowania, et cetera	Rosaceae	3
	Rhamnus	Rhamnaceae	1

TABLE 5

OLIGOLECTY IN CALIFORNICA GROUP OF PERDITA (PYGOPERDITA)
(Compiled from Timberlake, 1956)

Species	Pollen source	Region
P. calochorti Timberlake	*Calochortus nuttallii*	San Bernardino Co., Calif.
P. leucostoma Timberlake	*Calochortus leichtlinii*	Inyo Co., Calif.
P. californica (Cresson)	*Calochortus splendens*	Coastal central and Southern Calif.
	Calochortus kennedyi	
	Calochortus concolor	
P. montereyensis Timberlake	*Calochortus splendens*	Monterey Co., Calif.
	Eschscholtzia californica	
P. tularensis Timberlake	*Calochortus venustus*	Southern Sierra Nevada Mts., Calif.
	Calochortus luteus	
P. bispinata Timberlake	*Calochortus kennedyi*	Mojave Desert, San Bernardino Co., Calif.
P. macrostoma Cockerell	*Calochortus* sp.	Los Angeles Co., Calif.
P. bilobata Timberlake	*Calochortus aureus*	
	Calochortus kennedyi	Inyo and San Bernardino Co., Calif.
P. mohavensis Timberlake	*Eschscholtzia darwiniensis*	Mojave and Colorado Deserts, Calif.
	Eschscholtzia glyptosperma	
P. robustula Timberlake	*Eschscholtzia darwiniensis*	Colorado Desert, Calif.
P. argemones Timberlake	*Argemone* sp.	Arizona
P. arizonica Timberlake	*Calochortus* sp.	Coconino Co., Ariz.
P. distropica Timberlake	*Calochortus splendens*	Coastal central Calif.
	Eschscholtzia californica	
P. coalingensis Timberlake	*Eschscholtzia californica*	Fresno Co., Calif.
P. sculleni Timberlake	*Callochortus mutallii*	Utah
P. fallugiae Timberlake	*Fallugia paradoxa*	Charleston Mts., Nevada
P. cowaniae Timberlake	*Cowania stansburiana*	Panamint Mts., Calif.

half of them have been taken at Riverside on *Cryptantha intermedia.* As in the case of most generic oligolecty, *Proteriades* is morphologically adapted for the removal of pollen from this group of plants. However, Michener and Sokal (1957) have revised the concept of this genus and included certain elements not associated with *Cryptantha.*

The genus *Anthocopa* (Michener, 1943; Hurd and Michener, 1955) exhibits oligolecty at the level of the subgenus and species group. Thus *Atoposmia* is made up of species which take pollen from *Penstemon* (Scrophulariaceae), *Hexosmia* from *Phacelia* and *Nemophila* (Hydrophyllaceae), and *Eremosmia* breaks up into three groups, one of which utilizes pollen only from Compositae, the other two largely from Leguminosae.

The genus *Perdita* is one of the most striking groups of oligolectic bees (Cockerell, 1896). Table 4 summarizes oligolecty in most of the subgenera which have been recently revised by Timberlake (1954, 1956). Of particular interest is *Pygoperdita* which has its center of distribution in California (27 species), with five species known from Nevada, three each in Oregon and Utah, two each in Washington and Arizona, and one each in Colorado and Baja California. Timberlake (1956) recognized two species groups. The Interrupta group contains at least four species which obtain pollen from *Eschscholtzia,* one each from *Rhamnus* and *Adenostoma,* and five closely related species which collect from Compositae. The Californica group (table 5) included at least three species which gather pollen from *Eschscholtzia,* nine species from *Calochortus,* and at least two species which regularly take pollen from both.

Oligolecty and Entomophilous Flowers. In those regions where oligolecty is pronounced, the pollen flowers are usually scattered taxonomically through the local families of plants with entomophilous flowers. However, both Graenicher and Robertson have pointed out the special significance of the Compositae. In fact Graenicher (1935) considers it not only the largest but possibly the most important family with entomophilous flowers. Of the 921 flower species growing in Milwaukee Co., Wisconsin, he established 628 as entomophilous and 152 of these (24.2 per cent) were Compositae. The close grouping of the tubular florets in an inflorescence is especially attractive to bees, and he found that of 41 local oligoleges, 21 were associated with Compositae, especially fall-blooming species. He notes further that of the 54 species of Wisconsin oligoleges known to him, 20 were eastern in distribution and 34 exclusively or primarily western. Of these last, 19 are specific to Compositae which are largely characteristic of the western prairie flora.

Oligolecty in the Tropics. Michener (1954) states that for some reason, possibly connected with the relatively small seasonal variation in climate, there are few oligolectic bees in the American tropics as compared with any comparable faunal list from the temperate regions. His Panamá list contains several bees which belong to oligolectic genera (*Ancyloscelis* and *Melitoma* which obtain pollen only from *Ipomoea, Peponapis* only from *Cucurbita*). He suggests that these oligolectic bees arose in more arid areas, where competition for pollen is more intense, and later spread into the moist tropics.

The pollinating species usually cited for agricultural crops in tropical

areas are polylectic forms. Thus, Burkhill (1909) considers various species of *Xylocopa* to be the most important of the flower-visiting insects of tropical India (plains region) and largely responsible for the pollination of Sunn hemp and possibly Indian pulses. *X. latipes* Fabricius and *X. aestuans* (Linnaeus) visited 30 and 35 jute flowers per minute respectively. However, Maxwell-Lefroy (1909) cites *Lithurge atratus* Smith, presumably an oligolege of Malvaceae, as a persistent visitor of cotton plants in the same general region.

ADAPTATIONS ASSOCIATED WITH OLIGOLECTY

Ability to Locate the Appropriate Pollen Source. It has long been maintained that the bright colors of flowers were evolved for the visual attraction of pollinators (Lubbock, 1882; Müller, 1873) and that flower colors in the medium and ultraviolet ranges were particularly attractive to bees. Colors in the visual range of the bee (von Frisch, 1915; Kühn and Pohl, 1921; Kühn 1927)[8] no doubt serve a useful purpose in attracting the casual nectar seeker and together with the form and pattern of the flower, location on the plant, and certain other features may ease the task of the pollen collector and assist in pollen constancy (Lovell, 1909–1910, 1918). However, the only prior experience which the newly emerging solitary oligolege has had with its appropriate pollen source is the pollen and nectar which were stored by its parent. Presumably it must rely upon its olfactory and/or gustatory senses to guide it to the proper flower. The essential role of odor for insects which visit flowers was first emphasized by Plateau (1897, 1907) and the sensitivity of the olfactory organs of bees has been noted by various workers (McIndoo, 1914; von Frisch, 1919). Rayment (1935) reports that Australian tea-trees (*Leptospermum* spp.) are attractive (presumably by odor) to *Euryglossa fasciatella* Cockerell before the blossoms open, and G. E. Bohart (*in litt.*) has made similar observations of *Andrena* males and some females about *Salix*. Bees also recognize form in flowers (von Frisch, 1919; Hertz, 1929; Autrum, 1948, 1949). In addition, many flowers have *maculae indicantes,* the so-called "nectar guides" or "honey marks" (Sprengel, 1793) which guide the bee to the nectaries, and which may have a different scent from the rest of the flower

Michener (1953*b*) has shown that *Megachile brevis* Say, although taking pollen from plants as widely separated as the Leguminosae and Compositae, exhibits a preference for blue or purple flowers, and its principal sources are of these colors. Less important sources are white or greenish, and one minor source, yellow. Yet in the area where the study was made there are large numbers of yellow Compositae.

Leclercq (1945) has reported on the solitary bees which visited green hellebore (*Helleborus viridis* Linnaeus) in his garden. The petals and sepals of this flower are green, like the foliage, and its other features appear to mini-

[8] The color sense of bees is summarized by Grant (1950) and involves the perception of four main groups: (*a*) a yellow group which includes vermilion, orange, yellow, and yellow-green; (*b*); blue-green; (*c*) a blue group which includes blue, purple, and violet; and (*d*) ultraviolet. Bees are color blind for pure red. They distinguish different degrees of brightness as white, gray, and black but do not distinguish different shades within one color group.

mize visual contrast. It has no detectable odor, yet it was regularly visited by *Andrena albicans* (Müller), *Osmia cornuta* (Latreille), *O. rufa* (Linnaeus), *Halictus calceatus* (Scopoli), and *Bombus hypnorum* (Linnaeus), even in the presence of highly perfumed and brightly colored violets (*Viola tricolor* Linnaeus). At the same time it was consistently ignored by foraging honey bee workers and by both sexes of *Andrena fulva* (Schrank). Leclercq suggests that hellebore provides a particular scent to which bees are able to respond but which is outside the range of sensitivity of man. However, von Frisch (1919, 1921) has pointed out that the reactions of the olfactory organs of man and honey bees are much the same and that flowers which are odorless to us are also odorless to bees, although the latter can distinguish the scent of each species that has one. In the case of *Helleborus,* it is likely that bees recognize the ultraviolet color. Lotmar (1933) points out that red poppies (*Papaver*) are recognized by reflected ultraviolet light, and Hertz (1939) emphasizes that flowers that appear white to us are colored for bees and may look blue-green to them.

Leppik (1957) has discussed some aspects of the problem of evolutionary relationship between entomophilous plants and anthophilous insects. He concludes that the evolution of entomophilous plants has been controlled by insects (primarily bees) through the sensory behavior of the pollinators, that this selection tends to keep the evolution of flowering plants in a predetermined sequence, that various stages in the sensory development of pollinating insects are reflected in corresponding levels in the evolution of flower types, and develops a presumptive sensory mechanism which governs the food searching instincts of anthophilous insects and regulates their selective activity among flowers. Unfortunately, his argument is weakened by the fact that the literature and examples he cites pertain to the social bees (honey bees, bumble bees, stingless bees) and consideration is not given to the role of the solitary bees, numerically superior through time and space in both species and individuals. Further, the social bees are extremely polylectic, a large proportion of the solitary bees are oligolectic. Although visual and olfactory perceptions are known to be highly developed in social bees, little is known of their level in solitary bees. Also, Leppik takes no cognizance of the long series of morphological, physiological, and ethological adaptations of various oligolectic solitary bees to the plants which serve as their sources of pollen. Finally, of the bees to which he refers, only *Bombus* occurs naturally in the vast temperate flora of the Northern Hemisphere, and the size and weight of individual workers of most species in this genus limit their selective value to certain kinds of plants. If Leppik's thesis is correct, and I am not convinced that it is, the semisocial halictines may have assumed in the Northern Hemisphere, the selective role that he attributes to "bees." However, little is known regarding the level of sensory perception of this group or, for that matter, of polylectic solitary bees.

Seasonal Synchronization with Pollen Source. Synchronization of adults of certain bees with the blooming period of their host plant has been noted by many writers (e.g. Loew, 1884; Robertson, 1889, *et seq.;* Graenicher, 1909), mostly based upon observation and collections made at the flowers. However, studies of actual emergence of the bees from the ground in relation

to the appearance of the first bloom sufficiently abundant to be useful, has revealed that the degree of concurrence of the two events may vary considerably from season to season, not only with annuals and small perennials but also with flowering shrubs (Malyshev, 1936; Ulrich, 1933; Michener and Rettenmeyer, 1956; Linsley and MacSwain, 1957). However, most data thus far reported indicate reasonably close synchronization between oligolectic bees and their pollen sources. Possibly because of the limitations inherent in a single pollen source, the seasonal period of flight is usually shorter for oligoleges. Graenicher (1909) reports the average flight period for Wisconsin oligoleges as 44 days, for polyleges, 63 days, the latter flying 43 per cent longer. Robertson (1922) considered 85 per cent of the local Illinois Panurginae to be oligolectic, with flight periods averaging 53 days. Two species which were polylectic averaged 143 days (possibly more than one generation was involved). However, under desert and high montane conditions more extreme restriction may occur.

Since the preëmergence and prebloom environments of the bee and the flower are quite different, the physical and biological basis of synchronous timing is of considerable interest. Early spring bees (e.g. *Andrena*) usually overwinter as adults in the pupal cells in which they transformed. Most bees, however, overwinter as larvae and must pupate, transform, and harden before emergence. In either case these events take place from less than an inch to several feet below the surface, depending upon the species, and it is not clear how the bee and the flower can be attuned to the same stimuli. That moisture may be the key, at least in desert forms which overwinter as larvae, is suggested by Hurd (1957). He notes that *Geraea canescens*, a spring annual of the Mojave and Colorado deserts, bloomed in October, 1951, as a result of unseasonal rains of more than an inch. Its oligolege *Hesperapis fulvipes* Crawford, normally a spring bee, appeared at the same time. Since *Geraea* requires about an inch of rainfall for germination and since this amount of rain moistens the desert soil to a depth of from 18 to 24 in. (sufficient to reach the cells of the bee), a timing mechanism is available if the maturation process of the bee is initiated by moisture. In boreal areas, emergence of early spring forms which overwinter as adults appears to be associated with rising temperatures (Ulrich, 1933). However, this is also true in the case of *Nomia melanderi* Cockerell, and emergence of this species may be accelerated by placing polyethylene sheets over the ground and delayed by mulching the soil (G. E. Bohart, *in litt.*).

The short seasons of oligolectic bees have a tendency to provide concurrent variations in seasonal abundance of bee species. Graenicher (1909) recognizes two such peaks in Wisconsin; Stevens (1948), three peaks in North Dakota.

Seasonal Variation in Activity in the Tropics. In a tropical climate variations in the activity of animal life are at a minimum, but the variation is nonetheless considerable. Thus, in most parts of Panamá (Michener, 1954) there is a dry season beginning in mid-December and continuing to April or May. On the Pacific coast in the Canal Zone area, in spite of an annual rainfall in the vicinity of 60 in., the dry season is virtually without rain. In the early part of the dry season, while conditions are moist

but the days mostly clear and sunny, numerous herbaceous annual and perennial plants come up and bloom. It is at this season that bees known to have short seasons of flight can be found, and some of these appear to be intrusions from the north temperate regions (e.g. *Andrena vidalesi* Cockerell, *Calliopsis hondurasica* Cockerell).

Diurnal Synchronization with Pollen Source. Perhaps the most striking cases of synchronization with the pollen source are to be found among the crepuscular and matinal bees which gather their pollen after sunset or before sunrise. Many of these take their pollen from evening primroses (*Oenothera* and related Onagraceae). The best known of the semisocial crepuscular forms belong to *Sphecodogastra,* a subgenus of *Lasioglossum* (Halictidae), which has enlarged ocelli (almost universally associated with nocturnal habits in the bees) and a scopa modified for extracting the strands of pollen characteristic of onagraceous flowers. Four species are known, all of which collect pollen in the early hours of the night from evening primroses (Graenicher, 1911; Stevens, 1920). The group is closely related to the subgenus *Evylaeus,* which contains several species which gather pollen from diurnal Onagraceae and thus have the scopa similarly modified but have normal ocelli (Hurd, *in litt.*). A related neotropical halictine genus, *Megalopta,* also has large ocelli and Ducke (1902) records the capture of pollen-laden females at light at night in South America. Rau (1933) found a specimen of *M. genalis* Mead-Waldo in the laboratory on Barro Colorado Island, Canal Zone, at 6 a.m. Schwarz (1934) records 15 females and one male of this species taken at light at the same locality. However, pollen from four different plant species was being carried by different females indicating that this species, at least, is polylectic. The genus *Perdita* (subgenus *Xerophasma*) contains two large, pallid, nocturnal species with enlarged ocelli which collect pollen from *Oenothera* and are sometimes attracted to light (Cockerell, 1923; Timberlake, 1954).

Species of the eucerine genus *Xenoglossa* gather pollen from *Cucurbita* flowers before sunrise (Linsley, MacSwain, and Smith, 1956*a*), and the related genus *Peponapis* from sunrise until the flowers wilt or the pollen is exhausted. The andrenine subgenus *Onagrandrena* (see below) comprises bees which take pollen from *Oenothera* at dawn (Linsley, MacSwain, and Smith, 1955; Linsley and MacSwain, 1956). *Caupolicana yarrowi* (Cresson) another matinal species, was captured by Cockerell and Porter (1899) at flowers of *Datura* between 5:15 and 6:15 a.m. and Graenicher (1930) took a female during the same time of day at flowers of *Antigonon.* Schrottky (1907) made observations on two related South American species and concluded that on warm nights the bees are flying all night long. *Ptiloglossa* also contains matinal species and these have been observed in Mexico (Michener, *in litt.*) as well as in South America. *Lasioglossum lustrans* (Cockerell), an oligolectic halictine, is a matinal species which takes pollen only from *Pyropappus carolinianus,* the flowers of which close in the morning soon after the sun strikes them [Michener, 1947*a*]. The male of this species is considered by Michener to be as rigidly restricted in its flower visits as the female.

The Xylocopine subgenus *Nyctomelitta* comprises a number of nocturnal species with enlarged ocelli which inhabit the Indomalayan region. Of *X.*

(*N.*) *rufescens* Smith (= *X.* (*N.*) *tranquebarica,* Fabricius), Bingham (1897) states that on fine moonlight nights its buzzing can often be heard all night long. These species are, however, probably not oligolectic. E. S. Ross and H. B. Leech (*in litt.*) report finding the New World *Xylocopa rufina* Maidl visiting flowers in the dim light of dusk in the undergrowth of a pine forest on the south slope of Mt. Colima, Mexico, in December, 1948. Williams (1927), on the other hand, heard the introduced Hawaiian species of *Xylocopa* buzzing loudly among blossoms before sunrise, suggesting that the members of this genus are able to adjust broadly to local conditions of pollen availability. This appears to be true also of certain oligolectic forms. *Perdita* species of the *wootonae* group collect pollen from *Mentzelia* near sundown in Arizona and New Mexico in the fall. However, Timberlake (*in litt.*) found them active in the middle of the afternoon at Blythe, California, in April, apparently because the flowers open earlier at that time of year. Further, some bees appear to utilize the early hours of both morning and evening. MacSwain (1957) has recorded *Martinapis luteicornis* Cockerell taking pollen from *Cercidium* between 6:00 and 8:00 a.m. on the Colorado Desert, California, in April, and visiting *Dalea* between 4:00 and 6:00 p.m. in October.

Linsley and MacSwain (1958*c*) have called attention to the fact that the loud buzzing of matinal and crepuscular bees is only produced after sunset and before sunrise, suggesting a sonar-like device. These bees are commonly black or dark colored, permitting maximum heat absorption, a phenomenon that may explain the black desert bees of Peru (Cockerell, 1926).

Morphological Adaptations. Structural modifications associated with oligolecty are relatively numerous. Generally they involve adaptations which assist in the extraction and transportation of pollen or nectar or both. Such adaptations are frequently associated with group oligolecty. Thus, the species of *Verbenapis* have curled bristles on the front tarsi and are oligoleges of *Verbena.* The anthers of this flower are included in a slender tube with a circle of hairs above, which limits most bees to the extraction of pollen which adheres to the proboscis. However, *Verbenapis* thrusts both front legs into the corolla tube and extracts the pollen by means of the bristles on the front tarsi. On the other hand, the pollen of *Oenothera* (evening primroses) and other Onagraceae is difficult to collect because it is connected by threads. Oligoleges of these plants almost always have scopae composed of long simple bristles. This is true of such widely separated groups as *Anthedonia* (Robertson, 1914), *Diandrena* (Cockerell, 1937), *Onagrandrena* (Linsley and MacSwain, 1956*c*), *Diadasia* (Linsley and MacSwain, 1958*a*), *Anthophora,* and others, and seems to be an obvious specialization. Oligoleges of *Claytonia, Hibiscus, Geranium,* the Cactaceae and various other plant groups have loosely plumose scopae adapted to hold large pollen grains, those dependent upon the fine pollen grains of the Compositae have densely plumose scopae (Robertson, 1902).

Most members of such groups also exhibit physiological adaptations to their pollen plants. However, in *Proteriades,* morphological adaptations appear to restrict the pollen source regardless of other considerations. In all of the known species the galeae and labial palpi are provided with stiff curled hairs which are utilized to extract pollen from the stamens of *Cryptantha*

which are deeply hidden in the flower, but there is no evidence to suggest that the different species of *Proteriades* are restricted to different species of *Cryptantha* (Hurd and Michener, 1955). In fact the indications are that a species of *Proteriades* will utilize whatever *Cryptantha* species are available in the neighborhood. Hurd and Michener also state that there is no evident relationship between speciation in *Cryptantha* and that in *Proteriades,* and the distribution of the plant is far wider than that of the bee. Hurd and Michener (1955) point out further that in the vicinity of Riverside, where ten species of *Proteriades* are competing with one another on *C. intermedia* visiting the same flowers at the same season in the same place, the flight period of the bees does not even coincide with the main bloom of the *Cryptantha* plants.

Adaptations for the extraction of nectar from the pollen plant usually involve the length of the tongue (Taniguchi, 1954). They are most conspicuous in groups which collect pollen from plants with a deep corolla, and numerous examples are found among the higher bees. Included are such long-tongued anthophorines as *Ptilothrix, Melitoma,* and *Cemolobus* which take pollen from *Ipomoea,* the dufourine subgenus *Mimulapis* which utilizes *Mimulus,* the osmiine subgenus *Atoposmia* which visits *Pentstemon,* the andrenine subgenus *Iomelissa* which is restricted to *Viola,* and a great many others. *Chelostoma cockerelli* Michener, which takes pollen from *Eriodictyon* also has elongated mouthparts, but the species crawls into the flower and does not use them (Hurd and Michener, 1955).

Origin and Significance of Oligolecty. Lovell (1913) has said that the oligotropic habit is not beneficial to plants but concerns bees alone. However, it appears quite obvious that bees which as individuals or as a species collect pollen from only a few species of plants are likely to be more efficient pollinators than those which utilize many. From the standpoint of the bee, oligolecty probably enables it to avoid or reduce competition. Robertson (1914) believed that the bee fauna is all the flora will support, that there is constant competition between bees, and that natural selection favors those which are least competitive in the food habits (i.e. oligolectic). Lovell maintained that no satisfactory evidence has been produced to show that oligotropism is an effort by bees to avoid competition. He believed that if there were a scarcity of pollen sufficient to promise severe competition it would be a disadvantage to restrict visits to one kind of plant. However, since oligotropism clearly restricts competition between species, then, from the standpoint of a single species, in times of pollen shortage competition would be between members of each species, not with other species. By this means each species would be assured a minimum of food for its own survival (by means of a few successful individuals), whereas, if all species in time of shortage were competing for the pollen of all flowers, the less able would be exterminated. Oligolecty reduces competition by distributing the bees in space (on different kinds of flowers) and in time (in different parts of the year in accordance with the period of inflorescence of the flower or at different periods during the blooming period of the plant species). Thus oligolecty may be viewed as a mechanism for the preservation of a great many species which might otherwise fail to survive and may account for the large number of species existing in highly oligotropic

genera. In any one area, genera containing a high percentage of oligotropes possess many more species than those with a few oligotropes.

Michener (1953*a*, 1954) has pointed out that oligolecty is a form of host specificity. He comments that, in spite of the fact that polylectic species would appear to be at an advantage because they would be able to make use of more sources of food, their distributions would not be limited by those of a few hosts, and environmental changes which might eliminate the hosts and thus exterminate the oligolege might leave a polylectic species unaffected. Oligolectic species or groups of bees have arisen repeatedly from polylectic ancestors. From this it is obvious that specific adaptations must be advantageous as long as the proper environment is present. Such adaptations serve to get species out of competition with one another. He explains the mechanism thus:

"Among any group of polylectic species competing with one another for pollen supplies, one species will in all probability be at least slightly better adapted for obtaining its pollen from one flower, while others will be better adapted to other flowers. For example one species is better adapted for obtaining pollen from flower A than from other flowers, while a second species is better adapted to flower B. In this instance individuals of the first species visiting flower B will be at a disadvantage as compared to those visiting flower A because of the potent competition of the second on the flower to which it is best adapted. Therefore, the bulk of reproduction of the first species will be by individuals obtaining pollen from flower A, that is, selection will be against those visiting flower B. If, because of inherited characteristics or preimaginal conditioning, bees that visit flower A tend to produce offspring that visit flower A, there will be a tendency for the first species to restrict itself to flower A. Thus competition between the species is reduced. If, by a like process, the second species restricts itself to flower B, the two species are no longer in competition with each other."

However, although oligolecty may be beneficial to the species which exhibits it, it is not necessary that this be so. Like other adaptations it is probably perfected because of advantages provided to certain individuals of a species in competition with members of their own species.

Linsley and MacSwain (1958*a*, *b*) have emphasized that oligolecty, used in connection with a knowledge of mating habits, provides explanations for many evolutionary phenomena in the bees. To oversimplify, it permits the survival of large numbers of species in those groups which have this characteristic (e.g. most *Perdita*, many *Andrena*) by assuring that in years of pollen shortage, competition for what is available will be among members of the *same* species. In years when the appropriate pollen is completely lacking, the less adaptable species will become locally extinct, fragmenting the species geographically and setting the stage for geographic speciation resulting in closely related allopatric species with the same pollen plant (e.g., many *Andrena, Diadasia, Perdita*). With the breakdown of geographical barriers permitting these species to come together, the result is a group of closely related sympatric species with the same pollen plant. (If this situation is to remain relatively stable, some means will presumably be developed for lessening or minimizing the resultant competition for food; in *Onagrandrena* and certain species *Ptilandrena* this is accomplished by a partial division of the

diurnal period in which the pollen is available.) On the other hand, the adaptable species (for example, one without specialized pollen-collecting apparatus), or preadapted species, will presumably be able to change its food habits and, if the flowers are also the site for mating, isolation may become effective and provide a mechanism for speciation resulting in closely related sympatric species with quite different pollen plants. Thus, in *Diadasia,* although the majority of the North American species collect pollen almost exclusively from Malvaceae, *D. enavata* Cresson is restricted to Compositae, *D. angusticeps* Cockerell to Onagraceae and *D. bituberculata* Cresson to Convolvulaceae, suggesting sudden and abrupt changes in pollen hosts. The first two species exhibit morphological adaptations of the tibial scopa for the gathering and carrying of pollen grains from their respective sources. *D. bituberculata,* on the other hand, has elongated mouthparts suitable for extracting nectar from the deep flower of its pollen plant (*Convolvulus*). Linsley and MacSwain have shown that at least one species of *Diadasia* will turn to distantly related plants in the face of a local shortage of their usual pollen. They found a female of *D. australis* Cockerell taking pollen from *Phacelia* when that from the few available blooms of cactus (its regular source) had been exhausted.

Aside from its evolutionary significance, a knowledge of oligolecty is necessary for the intelligent assessment of bee species for possible introduction (Hurd and Michener, 1955).

INFLUENCE OF PHYSICAL FACTORS ON THE FLIGHT OF SOLITARY BEES

The complex of interacting physical factors which determines the periods of activity of a species of solitary bee has not been determined, and few precise data relating to the subject appear to be available. However, a few generalizations are possible. (Fig. 2.)

Sunlight. Generally speaking bees are sun-loving insects and in many species the shading of burrow entrances retards or alters activity. Even those species which are normally active early in the season (e.g., certain *Andrena*), when days are subject to the sudden appearance of clouds, will usually curtail activity or rest on the flowers when the sun is obscured. If the cloudy period is prolonged the females return to their burrows and the males may seek shelter. Since rain is detrimental to bees and can be disastrous to individuals trapped upon the flowers (Perkins, 1919), this behavior may be an adaptation to minimize this possibility. However, crepuscular and matinal species are often in flight during cloudy weather and social bees (*Apis* and *Bombus*) generally remain active if the temperature is not too low. In coastal areas subject to frequent fogs, species of *Andrena* that would not tolerate such conditions inland will remain active on foggy days (G. E. Bohart, *in litt.*).

Wind. Wind generally interferes with the flight of insects, but unless it is exceptionally strong or cold, most diurnal solitary bees will continue flight if the sun is bright, although their efficiency in the collection of pollen and nectar may be greatly reduced. Michener and Rettenmeyer (1956) state that

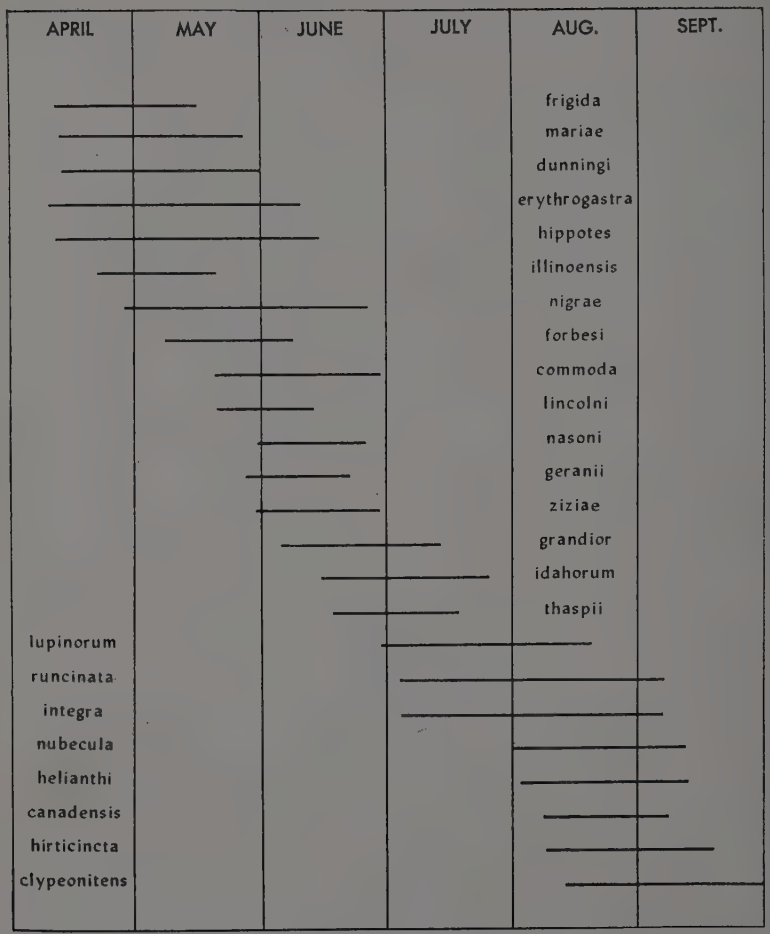


Fig. 2. Flight period of the commoner species of *Andrena* in North Dakota (extreme dates) (after Stevens, 1948).

Andrena erythronii Robertson is active even on windy days if the temperature is high. Robertson (1888) remarks that while wind requires bees to face it and thus alters their pattern of flight, it may compensate for this disadvantage by carrying the odors to them and by turning the flowers so that they are more easily seen and visited.

Temperature. Some data are available on the relation of temperature and the flight and activities of solitary bees. The most critical low temperature situations are faced by the bees with the earliest season (Ulrich, 1933).

Michener and Rettenmeyer (1956) have recorded certain temperatures in relation to the activity of *Andrena erythronii* Robertson, a species which flies so early that snow commonly falls after the first individuals have emerged. Apparently maximum air temperatures must be in the upper 50° F

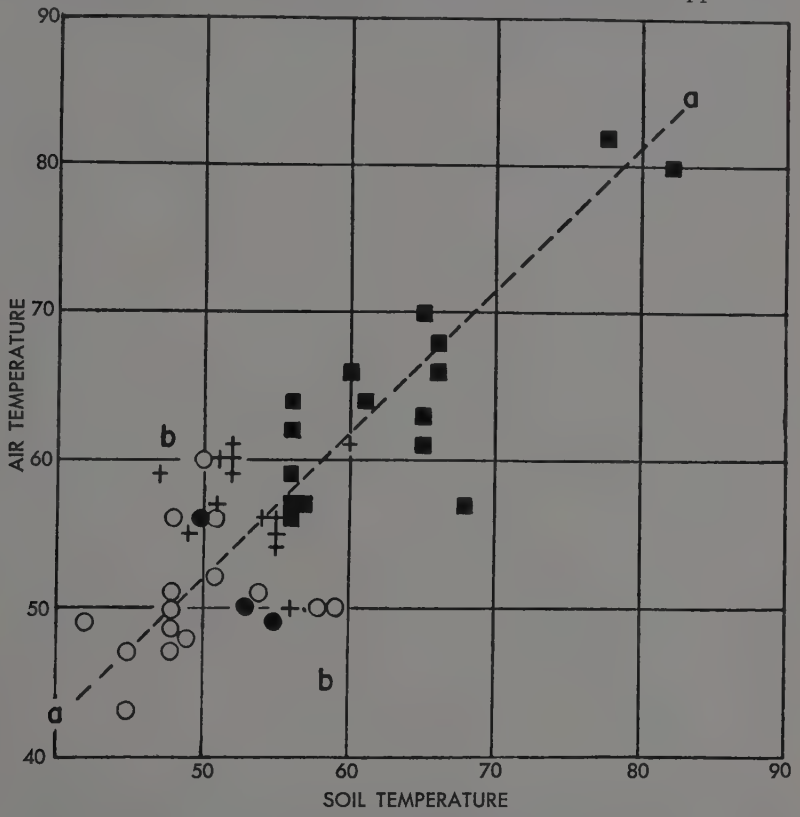


Fig. 3. Records of simultaneous air and soil temperatures (F) and activity of *Andrena erythronii*. Open circles indicate no activity. Squares indicate many bees flying. Beginning of activity is shown by closed circles (bees at surface but not flying) and crosses (only one or two flying in a 15-minute period). (Michener and Rettenmeyer, 1956.)

if flight is to occur, although occasional flights took place when air temperatures taken at the nesting places (in open shade ten centimeters above the ground) are 50° F. Even between 10:00 A.M. and 2:00 P.M., on clear or partly cloudy days, complete inactivity occasionally occurred at air temperatures as high as 60°; occasional, usually short, flights occur from 50° to 64°; while regular and extensive flights occur from 55° to 80°. These authors considered that variation in the type of activity which occurred at an air temperature of, for example, 55°, was caused by factors such as

surface temperature, soil temperature, wind, and light. Their data on surface and soil temperatures as would be expected, indicate that the range of surface temperatures is higher than the air temperatures, that of soil temperatures lower, when activity occurs. Since females survive later in the spring and thus into warmer weather than males, their temperature range extends higher. While both sexes are active the temperature factors influencing flight probably affect them similarly. The impression that males fly at lower temperatures was not supported by their data.

Simultaneous records of air and soil temperatures are summarized by Michener and Rettenmeyer in figure 3. They emphasize the occurrence of all the points about the line a-a (fitted by eye) reflects the expected correlation between air and soil temperature. The points indicating slight activity (crosses and solid circles) are concentrated in the region b-b, where the points are particularly widely scattered about the axis a-a. They suggest that this may be because slight activity often occurs at times of temperature change when the air temperature is rising above that of the soil or dropping beneath that of the soil.

Michener and Rettenmeyer were unable to find significant correlations between temperature or time of day and the duration of the pollen collecting trips of *Andrena erythronii*. However, Linsley and MacSwain (1946) noted an apparent relation between air temperatures and tripping rates for solitary bees visiting alfalfa.

Variations in temperature resulting from different exposures of nesting areas to the sun have, as would be expected, an influence on the diurnal and seasonal activity of bees. For example Vleugel (1947) states that in Holland aggregations of *Andrena vaga* Panzer on southeast slopes of dikes became active earlier in the spring, and the males disappeared earlier, than those on west slopes. Those on southeast slopes became active earlier in the morning and ceased activity earlier in the afternoon than those on west slopes. Unfortunately, he gave no actual temperature data.

INFLUENCE OF PHYSICAL FACTORS ON BEE POPULATIONS

The precise effects of physical factors of the environment on populations of solitary bees are not known. Most information on the subject is observational and, as in the case of the influence of physical factors on activity, precise data are generally lacking.

Low Temperature. Rau (1933) has correlated severe winters at St. Louis, Missouri, with marked reductions in local carpenter bee populations. He states that hedges of California privet at the Missouri Botanical Garden were killed by cold in the winters of 1917–18, 1923–24, and 1929–30, coinciding with years of low *Xylocopa* populations. Average temperatures for these winters were normal but minimum temperatures were very different. A minimum of 3° F was recorded for the winter of 1921–22 preceding a spring of *Xylocopa* abundance, a minus 13° F in the winter of 1929–30 preceding reduced populations (down 84 per cent in a group under observation).

Unseasonal Rainfall. Perkins (1919) has commented upon the disastrous effect of unseasonal rainfall on male bees, and Rau (1935) has described the destructive effects of heavy rainfall during the nesting period of *Andrena erythrogaster* (Ashmead). In the former case the bees were knocked to the ground and coated with mud or drowned. In the latter case the tumuli were beaten flat and the burrow openings covered with mud. Generally, however, excessive or unseasonal rainfall favors entomophagous or saprophagous fungi which destroy bees directly or indirectly in their burrows (Linsley and MacSwain, 1942*b*).

Cockerell (1936) reports that the winter and spring of 1934–35 were abnormally cool and wet in California and that the desert flora blossomed as it had not done for years. However, solitary bees were very scarce, and he comments on the paradox of weather which was so favorable to the plants but so unfavorable to the emergence and flight of their pollinators. Similar observations were made by the writer the same year at Los Angeles, and a rough attempt was made to correlate bee abundance with rainfall and other records during three successive seasons. The winter of 1934–35 was wet (21.66 inches rain); the next winter was unusually dry (12.7 inches rain), flowers were uncommon, yet bees were excessively numerous. During the winter of 1936–37, a record rainfall occurred (22.41 inches), the hillsides bloomed, and once again bees were very scarce.

The obvious explanation would seem to be that in years when flowers abound the bee fauna is so scattered that individuals are difficult to locate. This must, however, be only a partial explanation. Bees which are oligotropic visitors of perennial plants (except those xerophytic species which bloom sparingly or not at all in very dry years) should be more or less equally numerous in wet and dry seasons. This, however, does not seem to be the case, and many southern California bees which gather pollen only from *Salix, Ceanothus,* et cetera, are scarce in wet seasons. Likewise, if numerical variations were merely due to scattering, one would anticipate the same fluctuations in the numbers of honey bees encountered (allowing for commercial movements of apiaries, et cetera). Actually, although fewer honey bees are seen when flowers are plentiful (probably an effect of scattering) they are proportionately far more numerous than the solitary bees. Finally, colonies of *Andrena* which were under observation, were large and very active in 1936 (a dry season) and yet were reduced to a bare minimum in 1937 (possibly due to losses from molds).

The fact that in some situations a dry year following a moist one can result in large numbers of bees and a wet season after a dry one can have the opposite effect, suggests that in unfavorable years these bees wait over, remaining dormant in their burrows until a more favorable season. Since the fall and winter are normally passed as dormant larvae (in *Andrena,* however, as adults) this explanation does not seem unreasonable, and under laboratory conditions this actually occurs with some individuals. Another possible explanation is that in wet years, when flowers are more numerous, the bees can gather more pollen with less effort, making possible a large brood the following year. However, this would hardly apply in the case of species visiting perennials, as these usually nest near the plants and one

season is presumably no more favorable than another in this respect. Mean temperatures during the active period of the bees did not favor the spring season of 1936, and the number of cloudy days during the flight period which might be expected to exert an influence on the brood of the following year, was nearly as great in the wet spring of 1935 and the dry one of 1936, yet the broods of the following seasons were vastly different. It was therefore tentatively concluded that moisture probably has the greatest influence of any physical factor upon the seasonal abundance of early spring bees in the mild climate of the area. In arid regions, during years of no rainfall, emergence may be limited or prevented by dry soil conditions. When a nesting site of *Nomia melanderi* Cockerell in Utah dried up, many of the emerging bees had deformed wings and poor color (G. E. Bohart, *in litt.*).

PARASITES, PREDATORS, INQUILINES, AND FOOD DEPREDATORS

Among the many organisms which directly or indirectly destroy solitary bees, the majority are insects. Clausen (1940) has provided an excellent summary of information on most of these. Literature cited in this section is limited largely to papers which have appeared subsequently. For convenience the species will be discussed on the basis of whether they affect primarily the larvae or the adults.

Organisms Affecting the Larvae. Various creatures are intimately associated with burrows of solitary bees. Four principal groups can be recognized by the degree of parasitic or predatory relationship and the particular food habit (Linsley and MacSwain, 1958*a*): (*a*) those which in the first larval instar prey upon the egg and in subsequent instars feed upon the stored pollen and nectar; (*b*) those which parasitize or prey upon the developing or full-grown larva; (*c*) those which depredate the stored pollen and nectar and destroy, modify, or starve the larva to death; and (*d*) those which feed upon the contents of old cells and burrow refuse and only through accident have an adverse effect upon the host bee.

The first category includes several genera of so-called "parasitic," "cuckoo," or "inquilinic" bees (Friese, 1888; Wheeler, 1919; Richards, 1949; Grütte, 1935) and a few groups of meloid beetles (MacSwain, 1955). The bees oviposit directly in the cell of the host species, and the various genera are usually associated with definite host genera or groups (table 4) and the individual species may be highly specific. The meloid beetles do not oviposit directly in the cell of the host bee. Some (e.g. *Nemognatha, Zonitis*) place their eggs upon certain flowers and the newly hatched larvae cling to the bee as it visits the flower and are transported back to the nest (Linsley and MacSwain, 1952*a;* Selander and Bohart, 1954). Species in these genera may have few or many diverse hosts, depending in part upon the attractiveness of the plant selected to suitable bees. Others (e.g. *Tricrania*) oviposit in or near the nesting site and depend upon the larvae to attach themselves to a suitable host (Linsley and MacSwain, 1951). Although not host-specific, this habit further restricts the number of available hosts. A few (e.g. *Cissites, Hornia, Allendesalazaria*) oviposit in the natal cell or adjacent burrows

TABLE 6

ESTABLISHED AND PRESUMED GENERIC HOST RELATIONSHIPS FOR NORTH AMERICAN GENERA OF "PARASITIC" BEES*

(Extracted from Linsley and Michener, 1939; and Michener, 1944, with additions)

Family	Genus	Family or subfamily	Genus
Halictidae	*Sphecodes*	Halictidae	*Halictus*
		Halictidae	*Lasioglossum**
Megachilidae	*Stelis*	Megachilidae	*Heriades*
		Megachilidae	*Hoplitis*
		Megachilidae	*Osmia**
Megachilidae	*Chelynia*	Megachilidae	*Anthidium*
		Megachilidae	*Ashmeadiella**
		Megachilidae	*Heriades*
		Megachilidae	*Hoplitis*
		Megachilidae	*Osmia*
Megachilidae	*Diozys*	Megachilidae	*Callanthidium**
		Megachilidae	*Anthidium*
		Megachilidae	*Hoplitis**
		Megachilidae	*Diceratosmia**
		Megachilidae	*Osmia*
		Megachilidae	*Anthocopa**
		Megachilidae	*Megachile*
Megachilidae	*Coeliozys*	Megachilidae	*Megachile*
Anthophorinae	*Nomada*	Andrenidae	*Andrena*
		Halictidae	*Halictus*
		Halictidae	*Nomia*
Anthophorinae	*Hexepeolus*	Andrenidae	*Ancylandrena**
Anthophorinae	*Paranomada*	Anthophorinae	*Exomalopsis**
Anthophorinae	*Hesperonomada*	Anthophorinae	*Exomalopsis**
Anthophorinae	*Holcopasites*	Andrenidae	*Pseudopanurgus*
		Andrenidae	*Calliopsis*
Anthophorinae	*Neopasites*	Halictidae	*Dufourea*
Anthophorinae	*Townsendiella*	Halictidae	*Conanthalictus*
		Halictidae	*Hesperapis*
Anthophorinae	*Neolarra*	Andrenidae	*Perdita**
Anthophorinae	*Oreopasites*	Andrenidae	*Nomadopsis*
Anthophorinae	*Epeolus*	Colletidae	*Colletes*
Anthophorinae	*Triepeolus*	Anthophorinae	*Melissodes*
		Anthophorinae	*Svastra*
		Anthophorinae	*Anthophora*
Anthophorinae	*Epeoloides*	Melittidae	*Macropis*
Anthophorinae	*Melecta*	Anthophorinae	*Anthophora*
Anthophorinae	*Xeromelecta*	Anthophorinae	*Anthophora*
Anthophorinae	*Zacosmia*	Anthophorinae	*Anthophora*
Anthophorinae	*Ericrocis*	Anthophorinae	*Centris*
		Anthophorinae	*Anthophora*
	Mesoplia	Anthophorinae	*Centris*
Apidae	*Psithyrus*	Apidae	*Bombus*

* Presumed relationships are indicated by an asterisk (*). No data are available for *Heterostelis* (Megachilidae) or for *Triopasites, Melanomada, Protepeolus* or *Brachymelecta* (Anthophorinae).

and the larvae attach themselves to bees active in the site (Linsley and MacSwain, 1942c). This method not only greatly reduces the number of hosts but limits them to species of gregarious nesting habit. Such meloids are often highly host-specific.

The second category, comprising species which parasitize or prey upon the developing or full-grown larvae, is much more diverse. Two families of beetles (Rhipiphoridae, Stylopidae) are endoparasitic during all or part

of the larval development (Linsley, MacSwain, and Smith, 1952*b*; Linsley and MacSwain, 1957), and since the larvae gain access to the host on the flowers, the degree of host specificity, like that in *Nemognatha*, depends to some extent upon the nature of the visitors to the particular flowers concerned rather than to the nesting habits of the bee. However, within this range relatively high specificity is apparent. Among clerid beetles which place their eggs on flowers (e.g. *Trichodes*), some species use little discrimination in the kinds of flowers selected and thus infest a wide variety of bees and wasps with diverse nesting habits and exhibit little specificity (Linsley and MacSwain, 1944), and others seem to be more restricted (G. E. Bohart, *in litt.*). Certain meloids (e.g. *Meloe, Lytta*) oviposit in the soil in the nesting area. In the former genus the larvae climb plants and attach to adult bees, in the second genus they find their way into appropriate burrows. This habit restricts them to hosts which are abundant in a local site. Bombyliid flies (e.g. *Villa, Anthrax*), mutillid wasps (e.g. *Photopsis*) and certain mantispid neuropterans (e.g. *Plega*), oviposit in or near the burrows of their hosts and are commonly associated with gregarious species (Bezzi, 1924; Painter, 1932; Linsley and MacSwain, 1942, 1955). Larvae of the asilid genus *Hyperechia* are external parasites of *Xylocopa* (Poulton, 1924; Engel, 1929) and those of the sarcophagid genus *Brachioma* on bumble bees. *Metopia leucocephala* Rossi, however, occurs on *Lasioglossum pruinosum* (Robertson) (Melander and Brues, 1903). Sapygid wasps (Linsley, 1944*b*; Pate, 1947), chrysidids (Maneval, 1932; Hicks, 1933), leucospids (Graenicher, 1906*a*), and the pteromalid *Epistenia osmiae* (Ashmead) also oviposit in the cells of their hosts but are limited mainly to the solitary nests of megachilids, although within this group they are not usually species-host-specific and are often wide ranging geographically. Twig-nesting species (e.g. *Ceratina, Heriades, Hylaeus*) are especially susceptible to parasitism by Hymenoptera. Among the parasites involved in this habitat are *Gasteruption* (Höppner, 1904; Rau, 1928), the ichneumonids *Grotea* (Rau, 1922), *Holocryptus gracilis* (Provancher) (Viereck, 1916), *Melittobia* (Packard, 1865; Balfour-Browne, 1922), the torymid *Diomorus zabriskiei* Cresson and the eurytomid *Axima zabriskiei* Howard. The torymid genus *Monodontomerus*, however, parasitizes larvae of bees which nest in a variety of habitats and the related *Microdontomerus* is associated with the resin nests of *Dianthidium*. The diapriid *Acidopria columbiana* (Ashmead) infests the gregarious nests of *Lasioglossum pruinosum* (Robertson) (Melander and Brues, 1903).

Depredators on the larval food of bees include several genera of megachilids (e.g. *Stelis, Dioxys, Coelioxys*)[9] (Graenicher, 1905*b*, 1927; Michener, 1953*b*, 1955*a*; Popov, 1953; Hurd, 1958), ptinid beetles (esp. *Ptinus*) (Linsley and MacSwain, 1942), phorid flies (Borgmeier, 1925; Salt, 1929; Linsley, 1945), certain mites (Salt, 1929; Malyshev, 1931), and various kinds of molds (Linsley and MacSwain, 1942; Bohart and Cross, 1955). The latter are of common occurrence, but their role has not been evaluated. Several species of *Ptinus* occur regularly in bee nests and some of these are apparently associated primarily with species of *Osmia*. Bohart (1949) has recorded a fungus outbreak in adult bees. The mites associated with nests of solitary

[9] These, however, usually kill the bee larva at an early stage of development.

bees have not been well studied, but since they are transported on the bodies of the bees (Rayment, 1954*a*; Hirashima, 1957) they may be somewhat host-specific. Although the acarines in bees' nests have been generally regarded as food depredators, Lith (1957*b*) has shown that *Chaetodactylus osmae* (Dufour) and its relatives actually kill the bee larvae before turning to the stored pollen. Vitzhum (1930) has described seven species from nests of stingless bees.

Scavengers in the old burrows of solitary bees and sometimes on fresh pollen include dermestids (e.g. *Trogoderma, Anthrenus*), certain flies (e.g. *Hylemya cilicrura* Rondani, *Pegomyia affinis* Stein, and *Megaselia* spp.), moths (e.g., *Bitula, Tineola*), and various stored product pests (e.g., *Stegobium, Tribolium, Plodia*) (Linsley, 1942, 1944). Some of these (e.g., the dermestids) may open freshly provisioned cells and others (e.g., the flies) may infest newly stored pollen. In general, however, their activities are limited largely to sites of gregarious nesting species. Scavenging beetles are particularly numerous and varied in the nests of social bees (Salt, 1929; Plath, 1934).

Briefly, it would appear that the greater number of parasites, predators, depredators, and scavengers are associated with gregarious nesting, solitary bees, especially Anthophoridae, and that the most distinctive complex of parasitic forms is that associated with the Megachilidae.

Predators and Parasites of Adult Bees. Insect predators of adult bees belong largely to the robber fly family Asilidae and the philanthine and cercerine wasps of the family Sphecidae and the reduviid bugs of the Apiomerinae and Ectinoderinae, although many other groups are involved. The asilids (robber flies) are better known as predators of honey bees (Bromley, 1930; Hobby, 1931). Several genera (e.g. *Stenopogon, Diogmites, Promachus, Mallophora*, and *Proctacanthus*) commonly prey upon bees. In North America, *Promachus fitchii* Osten Sacken has been called the "Nebraska bee-killer." *Protacanthus milbertii* Macquart as the "Missouri bee-killer," *Mallophora orcina* Wiedemann and *M. bomboides* Wiedemann as the "Southern bee-killers" and *Saropogon dispar* Coquillett, *Diogmites angustipennis* Loew and *D. symmacha* Loew as "Texas bee-killers." Species of *Mallophora* and *Bombomima* are robust and hairy and resemble bumble bees, upon which they prey, but not exclusively. The former genus has been reported as an enemy of honey bees in Argentina and Cuba as well as North America. Among the North American species which prey to some extent on solitary and semisocial bees may be mentioned *Saropogon dispar* Coquillett (Halictidae, Andrenidae), *Diogmites texanus* Bromley (Halictidae), *D. symmachus* Loew (Anthophorinae, Andrenidae), *D. angustipennis* Loew (Halictidae), *D. umbrina* Loew (Andrenidae, Halictidae, Megachilidae), *Proctacanthus philadelphicus* Macquart (Anthophorinae, Andrenidae, Halictidae), *Promachus bastardi* Macquart (Halictidae), *P. fitchii* Osten Sacken (Andrenidae, Megachilidae, Halictidae), and *P. rufipes* Wiedemann ("solitary bees"), *Callinicus calceaneus* Loew (Megachilidae, Andrenidae) (Linsley, 1944*a*). The prey of 22 specimens of this last species were examined, and nearly three fourths consisted of brightly colored species of *Osmia*, the remainder of dull-colored *Andrena* spp., although the latter outnumbered the

former by about five to one on the flowers where the robber flies were capturing them (Linsley, 1944). G. E. Bohart (*in litt.*) reports that attempts to follow marked bees in Utah were interfered with by species of *Promachus* and *Proctacanthus* which swooped down upon the brightly marked individuals.

The Apiomerinae of the New World and Ethiopian region include many species which lie in wait for bees upon the flowers, capturing them by means of the front legs, aided by sticky materials. Miller (1956) comments that the habit of covering the anterior tibiae with a resin for the purpose of capturing prey is characteristic of some members of this subfamily. Specimens are often found to have a considerable amount of debris adhering to them on account of a glutinous material on their legs and body. Whether this substance is secreted by the insect or is deliberately collected by it is uncertain. The actual collection of a resinous substance by a member of this subfamily was observed in Surinam by Uittenboogaart (1901). With regard to the Ectinoderinae, Miller (1956) remarks that *Amulius* and *Ectinoderus,* which are found in the Oriental Region, make use of resins produced by certain trees which they smear on their anterior tibiae and utilize to capture small insects—usually bees of the genus *Trigona*—which become entangled like a fly on flypaper. Usinger (1958), in Thailand, reports *Ectinoderus longimanus* Westwood and *Amulius malayus* Stål lying in wait at the edges of resin pools in trunks of *Dipterocarpus alatus* for *Trigona* (*Tetragona*) *iridipennis* F. Smith, which swarmed about them.

Depredations of specid wasps of the genus *Philanthus* are best known in relation to honey bees (Fabre, 1891; Thiem, 1935; Olberg, 1953), and the common European species, *P. triangulum* Fabricius, is known as the "bee wolf." The wasps sting their prey in the throat which they then malaxate, feeding on the honey from the crop. The bee is then dragged to the burrow and stored in a cell with others to provide food for the larvae. The best known North American species, *P. gibbosus* Fabricius, provisions largely with halictines (e.g. *Augochlora, Halictus, Lasioglossum, Evylaeus, Curtisapis, Oxyglossa, Seladonia,* and *Dialonia*) but also utilizes the panurgid *Calliopsis andreniformis* Smith (Reinhard, 1924). The genus *Cerceris* is largely predaceous on Coleoptera (Linsley and MacSwain, 1955), but several species, including the European *C. rybiensis* (Linnaeus), prey upon halictine bees. Their habits are similar to those of *Philanthus,* and the females likewise perform extensive malaxation of the throat after stinging the prey (Maréchal, 1887). Other predators on adult bees include crab spiders and flower-inhabiting phymatid bugs (Balduf, 1939–43). In nesting sites they are also preyed upon by *Cicindela* tiger beetle larvae and adults (Frick, 1957).

Parasites of adult bees are almost exclusively flies. Among these are the phorid *Melaloncha ronnai* Borgmeier which oviposits in the abdomen of the bee during flight, and the larva destroys the bee and pupates in the thorax (Ronna, 1937). The sarcophagids *Senotainia* and *Myiapis* have similar habits (Seguy, 1930; Simintzis and Fiasson, 1951), the larvae feeding in the thorax. However, larvae of the tachinid *Rondanioestrus,* which larviposits on bees in flight, feed in the abdomen (Skaife, 1921). Probably the most important of the dipterous parasites of adult bees are conopids, which also

oviposit on the host in flight, destroy the body contents, and pupate in the dead shell. Most of the recorded hosts for European species and for several of the North American forms are bumble bees. However, *Physoconops* has been associated with *Megachile, Myopa* with *Andrena* and *Anthophora, Physocephala* with *Anthidium, Anthophora, Eucera, Megachile, Halictus, Bombus* and *Apis,* and *Zodion* with *Hylaeus, Panurginus, Nomia, Halictus* and *Apis* (de Meijere, 1903, 1912; Kröber, 1919; Camras and Hurd, 1957). In spite of the generic range of hosts, MacSwain and Bohart (1947) have reported indications of host specificity at the species level.

A symbiotic relationship apparently exists between laelaptid mites of the genus *Dinogamasus* (= *Dolaca*) and carpenter bees of the groups *Mesotrichia, Koptorthosoma, Platynopoda,* and *Cyaneoderes* (Vitzhum, 1930; Leveque, 1932). Nearly a dozen species are known to live in special pouches in the abdomen of female bees. The mites leave when nesting begins, enter the cells, and ultimately lay their eggs on the pupae. The larvae feed on exudations from the skin of the pupal bee and are mature by the time the bee transforms and they can enter the pouch (Skaife, 1952). The bees are apparently unharmed by the relationship and they derive no obvious benefit.

Role of Parasites and Predators in Population Control. Although local populations of solitary bee species are sometimes very large (Cockerell, 1933), little precise information is available indicating the role of parasites and predators in population control. What data have been published are largely expressed in terms of percentage of parasitism observed in samples taken from nesting sites or individual colonies of gregarious ground-nesting species, especially Anthophorinae (Linsley and MacSwain, 1942*b*), or twig-nesting forms, especially Osmiini (Medler, 1958). In large nesting sites, although the effects of parasitism are often noticeable, a wide variety of parasites may be tolerated. In the case of *Anthophora linsleyi* Timberlake, approximately 50 per cent of the larval progeny of a given season may be lost (table 7) without apparent detrimental effect upon the adult population which utilizes the site (Linsley and MacSwain, 1942*b*). In small sites, however, the right combination of parasites may be disastrous (table 8) and virtually exterminate a local population (Linsley and MacSwain, 1952*b*). However, the nature of the parasite or combination of parasites is more important than the size of the nesting site. Those which place their eggs on flowers are dependent upon the host bee visiting the flower and transporting the larvae to the nest. Thus, *Rhipiphorus smithi* Linsley and MacSwain, which oviposits on *Sida,* the pollen source for *Diadasia consociata* Timberlake, has a relatively long season and can infest from 15 to 30 per cent of the cells in a given area (Linsley, MacSwain, and Smith, 1952*a,* 1952*b*). *Zonitis atripennis* (Say), which oviposits on *Cleome* in certain areas, may have been an equally heavy parasite on *Nomia melanderi* Cockerell. However, *Nomia* now prefers introduced alfalfa and sweet clover, and in places where these are available parasitism by *Zonitis* is generally less than one per cent (Selander and Bohart, 1954). Potentially, the most effective insect parasites of gregarious ground-nesting species are probably bombyliid flies which in a *Nomia* colony are capable of infesting almost 100 per cent of the burrows which are open at a given time (G. E. Bohart, *in litt.*). However, although

in this case the fly *Heterostylum* begins activity at the same time as *Nomia melanderi* Cockerell, the season of the latter is a little longer and thus the local population is able to avoid extermination. *N. triangulifera* Vachal, which nests in the same areas but starts its season late is only lightly parasitized. Thus timing is an important factor in maintaining this, as other host-parasite relationships. Stephen (1958), observing that the mature larvae of *Heterostylum robustum* Osten Sacken, the chief parasite of *Nomia me-*

TABLE 7

PARASITES, PREDATORS, AND SCAVENGERS IN NESTS OF ANTHOPHORA LINSLEYI TIMBERLAKE AT TWO CALIFORNIA LOCALITIES
(After Linsley and MacSwain, 1942*b*)

	Nr. Little Lake Inyo Co., Calif.		Nr. Bakersfield Kern Co., Calif.	
	No. of cells	Per cent of total	No. of cells	Per cent of total
Cells examined	1920	100.00	759	100.00
Living *Anthophora*	909	47.34	370	48.75
Mold-killed *Anthophora*	203	10.58	...	
Hornia boharti Linsley (Meloidae)	458	23.85	111	14.62
Trogoderma simplex Jayne (Dermestidae)	118	6.14	40	5.27
Xeromelecta californica Cresson (Anthophorinae)	75	3.91	44	5.79
Nemognatha scutellaris LeConte (Meloidae)	6	.31	44	5.79
Anthrax nidicola Cole (Bombyliidae)	76	3.96	33	4.34
Photopsis auraria (Blake) (Mutillidae)	42	2.19	19	2.50
Photopsis sercus Viereck (Mutillidae)	...		1	.13
Hylemya cilicrura Rondani (Anthomyiidae)	20	1.04	...	
Ptinus californicus Pic (Ptinidae)	..		32	4.21
Lytta occipitalis Horn (Meloidae)	..		11	1.45
Lytta purpurascens Fall (Meloidae)	..		29	3.82
Lytta chloris Fall (Meloidae)	..		7	.92
Monodontomerus montivagus Ashmead (Torymidae)	5	.26	4	.52
Triepeolus mojavensis Linsley (Anthophorinae)	..		3	.39
Chrysis (*Chrysis*) sp. (Chrysididae)	..		3	.39
Chrysis sp. (Chrysididae)	..		3	.39
Plodia interpunctella (Hübner) (Pyralidae)	..		3	.39
Tineola biselliella Hummel (Tineidae)	..	...	2	.26
Oryzaephilus surinamensis (Linnaeus) (Cucujidae)	5	.26	...	
Gen. et sp. incert. (Ichneumonidae)	2	.10	...	...
Stegobium paniceum (Linnaeus) (Anobiidae)	1	.05	...	...

landeri Cockerell in Oregon, move upward out of the bee cells and spend some time in the top few inches of the soil, obtained excellent control of the flies by rototilling the soil with an insecticide and then packing the soil down. Rototilling and packing were reasonably effective even without the insecticide.

Parasites which oviposit in the nests of nongregarious species (e.g. *Coelioxys, Stelis, Nomada*) learn to recognize certain nests and return to them repeatedly (Graenicher, 1906*b*; Michener, 1953*b*, 1955; Linsley and MacSwain, 1955*a*) resulting in a very high percentage of parasitism in certain nests and cell series, a complete absence of parasites in others. Also, the searching pattern of such species may limit the nests which can be parasitized. *Coelioxys octodentata* Say is an important parasite of *Megachile brevis* Say, a species which nests commonly in dead stalks but also in other habitats as

holes in wood or soil, under stones, matted grass, et cetera. However, Michener (1953*b*), in the course of a careful study of the host species, observed *Coelioxys* searching only dead stalks and no parasitized cells were found in any other habitat.

The role of predators and parasites of adult solitary bees in controlling population levels is equally unclear. Bromley (1930) concludes that robber flies can rarely cause economic losses to apiarists because they are rarely

TABLE 8

PARASITES AND PREDATORS IN NEST SAMPLE FROM A SMALL POPULATION OF DIADASIA BITUBERCULATA (CRESSON)
(After Linsley and MacSwain, 1952*b*)

	No. of cells	Per cent of total	Per cent of non-moldy cells (248)
Cells sampled	377	100.0	100.0
Unparasitized *Diadasia:*			
overwintering larvae	32	12.5	
adults	15		21.8
Adult *Diadasia* dead from unknown causes	7	1.9	
Cell contents destroyed by molds	129	34.2	
Villa (*Paravilla*) *tricellula* Cole (Bombyliidae)			
larvae	84		
pupae (including 7 dead)	18	27.1	41.1
Rhipiphorus diadasiae Linsley and MacSwain (Rhipiphoridae)			
larvae (endoparasitic first instar)	12		
pupae	2	12.1	18.5
adults (including 26 dead)	32		
Photopsis auraria Blake (Mutillidae)			
larvae	5		
pupae	8	5.3	8.1
adults (including 3 dead)	7		
Photopsis sp. (Mutillidae)			
larvae	11	2.9	4.4
Lytta melaena LeConte (Meloidae)			
larvae	11	4.0	6.1
pupae	4		

abundant enough. However, Clausen (1940) states that the reduction in populations of wild bees through attacks of various species of Asilidae may have injurious results because of less complete pollination of blossoms. Ronna (1937) records losses of up to 50 per cent of adult bees from attacks by the phorid *Melaloncha* in Brazilian apiaries but what the losses might be to solitary bees under less concentrated conditions is not known. Clausen (1940) states that the comparative scarcity of the Conopidae gives them relatively little importance, although he grants that their attacks on bumble bees may reduce pollination. However, Bohart and Cross (1955), in part, attribute deceleration in nest construction by *Nomia melanderi* Cockerell to para-

sitism of adult females by larvae of *Zodion obliquefasciatum* Macquart, the developing larvae of which progressively starve the ovaries and then crowd them out.

The Effects of Parasitism on Behavior of Bees. Most of the parasites of adult bees have visible effects upon the behavior of their hosts, but none have been so thoroughly studied as those of the genus *Stylops* in bees of the genus *Andrena* (Pérez, 1886; Pierce, 1909; Wheeler, 1910; Smith and Hamm, 1914; Perkins, 1918; Salt, 1927, 1931; Clausen, 1940; R. M. Bohart, 1941). These parasites frequently bring about reduction in the size of the head, enlargement of the abdomen, disturbances in wing venation, abnormal puncturation and pilosity, and a reversal of the secondary sex characters. Sexual dimorphism is normally very pronounced in *Andrena*. The males may have a larger head with a yellow clypeus; always possess an additional segment in the abdomen and usually in the antennae; and slender legs which are devoid of pollen-collecting apparatus, et cetera. Any reversal of secondary sexual characters is pronounced, and a conspicuous intersex may be produced. Internal effects of stylopization mainly involve the gonads. In the female these are usually reduced to a point where the bee is incapable of reproduction. In the male, the reduction usually involves only one side, and ripe sperm still may be available. In general, the parasitized forms emerge early, permitting mating, eclosion of the eggs and larviposition on the flowers to take place in time for the main pollen collecting season of the host. Usually the sex instinct is not destroyed in either the male or the female, although the latter is usually incapable of reproduction. The pollen collecting instinct is usually lacking, although the bees frequent flowers and thus infect them with parasite larvae. All of the effects of stylopization are increased when the parasite is a male, regardless of the sex of the host. Smith and Hamm regard it as possible that the presence of the male *Stylops* (since it undergoes complete metamorphosis) has a more generally damaging effect on the bee, but there is no evidence of the male parasite exciting a specific male effect and the female exciting a female effect upon the host. Salt, in an extensive study of the effects of stylopization, explains them on the basis of nutrition. He points out that stylopized bees are intersexes, and that presumably the abstraction of nourishment by the parasite removes essentials from the host which upset the reaction of hormones. His assumption is based on the fact that in *Andrena* the effect of the male parasite is greater than the female (apparently the result of the extraction of more nutritive material from the host). In *Polistes,* however, where the larvae are fed progressively and not forced to survive upon a limited amount of food, the effect of the male parasite is no greater than that of the female (apparently because the larvae were given sufficient food to offset that required by the parasite).

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